Rules for Posture Selection

Cognitive principles of human motor control

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Contents

General Introduction

CHAPTER 1

The Process of Sensorimotor Integration

For even the simplest movements we conduct, our sensory input and motor output are closely interwoven. Our movements are planned and executed based on sensory input, and sensory input in return is affected by our movements. Pioneering work on the influence of sensory input on movement execution was done by Woodworth (1899). In his study, participants had to conduct back-and-forth movements between two predefined locations with a stylus, both with and without visual feedback. In the visual feedback condition, movement error decreased as movement velocity decreased, whereas movement error was constant without visual feedback. This result proved that sensory input from the visual system is used to correct the ongoing movement. Based on the velocity value at which the error graphs of both feedback conditions diverged, Woodworth estimated a critical movement duration of 200 ms for visual feedback to affect the movement. Similar results were replicated by Keele and Posner (1968). Later research, however, showed that visual feedback takes less than 100 ms (Zelaznik, Hawkins, & Kisselburgh, 1983).

Conversely, sensory input is influenced by the own movements. Head and eye movements, for example, result in a shift of the retinal image. This shift, though, is not perceived as a movement of the environment. The central nervous system thus can distinguish between sensory changes caused by own movements and sensory changes caused by external stimuli. A proposed mechanism for this distinction is the *reafference principle* (Helmholtz, 1867). Each motor command (efference) is accompanied by a second signal (efference copy), which encodes information about the sensory effects of the movement (reafference). The efference copy is subtracted from the sensory input (afference) and, thus, cancels out the reafference, leaving only external stimuli (exafference). Von Holst and Mittelstaedt (1950) provided convincing evidence for the reafference principle by exploiting the optokinetic reaction of flies (*Eristalis spec.*). Internal subtraction processes, however, have also been attributed to other species, including humans (Sperry, 1950; Wolpert & Flanagan, 2001). Robust demonstrations of the reafference principle prove that sensory input is affected by movements. They further show that, even for apparently motor-unrelated, perceptual processes, the sensory effects of the own movements have to be anticipated.

Effect Anticipation and Ideo-motor Theory

The functional role of sensory effect anticipation in motor control has been addressed in a number of current theories of cognitive psychology. For instance, the *cognitive-perceptual approach* (Mechsner, 2004; Schack & Mechsner, 2006; Schack & Ritter, 2009), the *theory of event coding* (Hommel, Müsseler, Aschersleben, & Prinz, 2001), and its precursors (Hommel, 1997; Müsseler, 1999; Prinz, 1992, 1997) integrate elements of *ideo-motor theory*. The theory states that movements are selected and initiated by their anticipated sensory effects (Greenwald, 1970). This concept can be traced back to the nineteenth century (Carpenter, 1852; Harleß, 1861; James, 1890; Lotze, 1852) but was suspended during the area of behaviourism (Thorndike, 1911). Ideo-motor theory presumes a bidirectional association of movement and sensory effect. Each movement has to be associated with its ensuing effect. Thus, the effect of the movement can be anticipated (Elsner & Hommel, 2001). This *action-effect learning* was proposed by Herbart (1825) and has been demonstrated experimentally for instance by Hoffmann and colleagues (2001). In the inverse direction, each effect has to be associated with a movement. Thus, an intended effect can initiate a corresponding movement. The neurophysiological mechanism for this bidirectional link has been described by *Hebbian learning* (Hebb, 1949), which states that the synaptic strength between two neurons increases if both are active at the same time. Effect-induced initiation of a movement was demonstrated in a study by Elsner and Hommel (2001). In a training phase, participants performed button presses, which produced different auditory effects. In a subsequent test phase, these auditory effects were used as stimuli. In a choice reaction task, movements were initiated faster if triggered by their associated effects. In a free choice task, movements were selected more often if triggered by their associated effects (Elsner & Hommel, 2001). These findings demonstrated that the associated effect facilitates both the initiation and selection of a movement. Even more convincing support for this facilitation was provided by Kunde (2001). Previous research on *stimulus-response compatibility* showed that, in a choice reaction task, movements were initiated faster if triggered by a compatible stimulus (Fitts & Seeger, 1953; Simon, 1969; Simon, Hinrichs, & Craft, 1970). Kunde reasoned that, if movements were initiated by their anticipated effects, a comparable *response-effect compatibility* should be present if a movement resulted in a compatible effect. Such response-effect compatibility has been successfully demonstrated for effect location (Kunde, 2001), intensity (Kunde, 2001), and duration (Kunde, 2003). These results prove that a representation of the anticipated effect is active before the movement is initiated.

The Redundancy Problem

The concept of effect anticipation has not only been addressed in early physiology (Helmholtz, 1867; von Holst & Mittelstaedt, 1950) and psychology (Herbart, 1825; James, 1890; Lotze, 1852), but can also be found in the pioneering work on movement science by Bernstein (1967). Bernstein hypothesised that movements are selected in order to realise biological requirements of the organism in the external world. For this purpose, the organism extrapolates different models of the future, depending on its movement alternatives. Bernstein is, however, most renowned for defining a central problem of sensorimotor integration, the *redundancy problem* (Bernstein, 1967). Even a simple reaching movement to an object in three-dimensional space requires a series of coordinate transformations between the sensory system and the motor system. Due to the large number of independent degrees of freedom of the movement system, several motor transformations have infinitely many valid solutions. The object location, for example, can be reached by different hand paths. Each hand path can be realised by different postures. Each posture can be achieved by different muscle activation patterns. The redundancy problem highlights a potential shortcoming of ideomotor theory, which presumes a bidirectional association of a movement and its sensory effect. Motor commands consistently result in the same sensory effect and, thus, can be associated with this effect through Hebbian learning (Hebb, 1949). Both the pre- and postsynaptic neurons are coactive each time the motor command is executed, which results in an increase of the synaptic strength. Based on the same mechanism, the efference copy (von Holst & Mittelstaedt, 1950) can be associated to the reafference. In the opposite direction, however, the same sensory effect can be achieved by an infinite number of different motor commands. The probability that the same pre- and postsynaptic neurons are coactive is therefore low and the synaptic strength cannot increase. Thus, in order to work, the ideo-motor theory requires an intended effect to consistently result from the same, reproducible motor command. To this end, the motor system has to solve the *ill-posed problem* (Jordan & Wolpert, 1999) of selecting a single solution from the multitude of valid solutions for each motor transformation. Movement planning therefore adds up to the evaluation of computational rules for this selection process. Experimental observations of aimed limb movements indicate that such selection rules exist, since several kinematic parameters remain invariant, independent of movement direction, speed, and location (Atkeson & Hollerbach, 1985; Flash, 1987; Hogan, 1984). Hand path, for example, follows a roughly straight line in space and exhibits a smooth, bell-shaped velocity profile (Flash & Hogan, 1985; Morasso, 1981; Soechting & Lacquaniti, 1981). A direct computational approach for movement evaluation and selection is provided by optimisation theory (Jordan & Wolpert, 1999). Multiple time-varying values, which describe the movement, are compressed into a single optimality measure, such as minimum jerk (Flash & Hogan, 1985; Hogan, 1984), minimum torque change (Uno, Kawato, & Suzuki, 1989), minimum energy (Holt, Hamill, & Andres, 1990), or minimum end-point variance (Harris & Wolpert, 1998; Jordan & Wolpert, 1999; Rossetti, Meckler, & Prablanc, 1994). Computational models based on these criteria reliably reproduce the hand trajectories demonstrated by experimental observation (Flash & Hogan, 1985; Harris & Wolpert, 1998; Uno et al., 1989). To simplify the computational models, however, arm movements in all studies were restricted to the horizontal plane. This restriction resulted in a unique mapping of target location and arm posture. Optimality models thus did not address the redundancy problem of posture selection.

Motor Primitives as Basic Units of Movement

A ground-breaking idea for the solution of the redundancy problem was proposed by Bernstein (1967). He suggested that multiple degrees of freedom should be combined into a single *movement synergy* or *motor primitive*. Degrees of freedom in a motor primitive are no longer independent but coupled in their action. Each motor primitive constitutes a basic unit of movement, which is controlled by a single motor command. Motor primitives thus reduce the number of independent degrees of freedom. Temporal couplings between multiple degrees of freedom were first described for contra lateral limb movements of vertebrates (von Holst, 1939). Movement synergies have been reliably demonstrated for muscle activity in frog hind legs (d'Avella & Bizzi, 1998, 2005; d'Avella, Saltiel, & Bizzi, 2003). In human subjects, muscle synergies have been identified in a centre-out pointing task: Five synergies explained most of the data variance of the muscle activation patterns and their amplitude coefficients were directionally tuned according to a cosine function (d'Avella, Portone, Fernandez, & Lacquaniti, 2006). Similar results were demonstrated for muscle synergies in the wrist joint (Haruno & Wolpert, 2005). Neurophysiological studies, on the other hand, rather support a postural approach of motor control (Scott, Gribble, Graham, & Cabel, 2001; Scott & Kalaska, 1997). Graziano and colleagues (Graziano, Aflalo, & Cooke, 2005; Graziano, Taylor, & Moore, 2002) showed that microstimulation of the motor cortex in monkeys evoked complex final postures, regardless of movement direction and joint torques. The authors thus demonstrated that not only muscle activation patterns but also postures are encoded in the motor cortex. Postural motor primitives were demonstrated for the hand in several studies (Gentner & Classen, 2006; Grinyagin, Biryukova, & Maier, 2005; Santello, Flanders, & Soechting, 1998). Santello and colleagues (1998), for example, found that two motor primitives captured most of the data variance of hand postures when grasping familiar objects. A large number of studies identified postural motor primitives of unrestrained arm movements (Berret, Bonnetblanc, Papaxanthis, & Pozzo, 2009; Bockemühl, Troje, & Dürr, 2010; Debicki & Gribble, 2005; Latash, Aruin, & Shapiro, 1995; Sabatini, 2002; Thomas, Corcos, & Hasan, 2005). Bockemühl and colleagues (2010), for example, showed that three motor primitives explained most of the data variance of arm postures in an unrestrained catching task. These results demonstrated that motor primitives efficiently reduce the number of independent degrees of freedom of the movement system. However, target locations in all mentioned studies were restricted to two-dimensional planes, but a minimum of three motor primitives was required to capture most of the data variance. This signifies that, even after the number of independent degrees of freedom had been reduced, at least one redundant degree of freedom remained. Thus, motor primitives alone are not sufficient to solve the redundancy problem of posture selection in reaching and catching tasks. Additional rules are required to select a single solution for the transformation between target location and posture. The line of research presented in the current thesis focuses on the investigation of different rules for posture selection.

Rules for Posture Selection

A major step towards a better understanding of posture selection was made by the comprehensive work of Rosenbaum and colleagues (Rosenbaum & Jorgensen, 1992; Rosenbaum et al., 1990). The authors identified two fundamental rules for posture selection, the *end-state comfort effect* (Rosenbaum et al., 1990) and *sequential effects* (Rosenbaum & Jorgensen, 1992).

End-state Comfort

In the first study on posture selection by Rosenbaum and colleagues (1990), participants had to grasp a horizontal bar and place one end on a target disk. Results showed that participants selected different initial postures depending on which end they intended to place on the target. By adopting an awkward initial posture (i. e. an underhand grasp), participants avoided ending their movements in an awkward final posture. This behaviour was termed the *end-state comfort effect* (Rosenbaum et al., 1990). The end-state comfort effect has been reliably reproduced in a series of experiments (Cohen & Rosenbaum, 2004; Hughes & Franz, 2008; Hughes, Reißig, & Seegelke, 2011; Seegelke, Hughes, & Schack, 2011; Short & Cauraugh, 1997, 1999; Weigelt, Cohen, & Rosenbaum, 2007; Weigelt, Kunde, & Prinz, 2006). Sensitivity to end-state comfort has been shown to develop over the lifespan (Stöckel, Hughes, & Schack, 2011; Weigelt & Schack, 2010). In order to achieve end-state comfort, the terminal posture has to be anticipated before the movement is initiated. Similar effects were described in studies on ideo-motor theory: The anticipated effect of a movement facilitates both its selection and initiation (Elsner & Hommel, 2001).

Kunde (2001) further proved that the representation of an anticipated effect is active before the movement is initiated. A number of different explanations have been postulated for the end-state comfort effect, such as the minimisation of time spent in awkward postures, the exploitation of potential energy (Rosenbaum & Jorgensen, 1992), and the precision hypothesis (Rosenbaum, van Heugten, & Caldwell, 1996). The precision hypothesis, for example, states that it is easier to make positioning movements at or near the middle of the range of motion than near the extremes (Rosenbaum et al., 1996). Several experiments support the precision hypothesis as a driving factor behind the end-state comfort effect (Rosenbaum, Halloran, & Cohen, 2006; Rossetti et al., 1994; Short & Cauraugh, 1997, 1999). The impact of precision demands on the anticipation of a subsequent movement has also been demonstrated for prehension (Ansuini, Santello, Massaccesi, & Castiello, 2006; Armbrüster & Spijkers, 2006; Gentilucci, Negrotti, & Gangitano, 1997; Marteniuk, MacKenzie, Jeannerod, Athenes, & Dugas, 1987). For example, the hand velocity profile of a prehension movement varies depending on whether the grasped object subsequently has to be thrown or placed (Armbrüster & Spijkers, 2006; Marteniuk et al., 1987). Both the shape of the hand and the finger positions on the grasped object differ depending on the subsequent precision demands of the task (Ansuini et al., 2006). Hesse and Deubel (2010) further demonstrated that the target orientation of an object affects the initial hand orientation, but also showed that this anticipation is lost if an intermediate task with high precision demands is introduced.

Sequential Effects

Many of the previously mentioned findings on posture selection were concerned with discrete motor acts. Participants completed a single object manipulation per trial. In daily life, however, tasks are carried out in the context of ongoing sequences of behaviour. The first experiment on such *sequential effects* in reaching was done by Rosenbaum and Jorgensen (1992). Participants were asked to grasp a horizontal bar and to place its left or right end against one of 14 vertically aligned targets in a sequential order. Results showed that, for the middle targets, participants tend to select the previous grasp posture (overhand vs. underhand). This persistence is restricted to a *range of indifference*, where participants are equally content with either posture (Rosenbaum, Cohen, Jax, Weiss, & van der Wel, 2007; Rosenbaum & Jorgensen, 1992). Within this range, a new movement plan can be created by modification of the former plan. The modification causes lower cognitive costs than the creation of a new movement plan from scratch (Rosenbaum et al., 2007). Sequential effects thus constitute a rule to reduce the cognitive costs of movement planning in a sequential task. Persistence to a previous movement has been demonstrated for the hand path in a number of studies (Diedrichsen, White, Newman, & Lally, 2010; Jax & Rosenbaum, 2007; van der Wel, Fleckenstein, Jax, & Rosenbaum, 2007). Passive guidance of the hand in a task-redundant dimension, for example, induces a lasting modification of the hand path (Diedrichsen et al., 2010). Modifications of the posture are a prerequisite for such a modification of the hand path. Several studies have reliably reproduced sequential effects of posture selection (Kelso, Buchanan, & Murata, 1994; Rosenbaum & Jorgensen, 1992; Weigelt, Rosenbaum, Hülshorst, & Schack, 2009). For example, when opening a column of drawers in a sequential order, the transition point between overhand and underhand grasp shifts depending on the movement direction (ascending vs. descending; Weigelt et al., 2009). In contrast to the end-state comfort effect, sequential effects do not constitute a posture selection rule per se. Instead, they can be considered a meta rule that is used to decide between the reuse of a previous posture and the selection of a new posture.

Research Questions and Hypotheses

In the current thesis, three rules that contribute to the selection of postures are addressed: (1) the *end-state comfort effect*, which indicates the selection of a comfortable terminal posture, (2) *sequential effects*, which imply the reuse of a previous posture, and (3) *motor primitives*, which efficiently reduce the number of available postures.

Transfer of Posture Selection Rules to a Continuous Task

The end-state comfort effect and sequential effects of posture selection have been reproduced in a large number of studies (Kelso et al., 1994; Rosenbaum & Jorgensen, 1992; Rosenbaum et al., 1990; Short & Cauraugh, 1997, 1999; Weigelt et al., 2006, 2009). To simplify the description of the selected posture, a majority of these studies were restricted to binary tasks (e. g. overhand vs. underhand grasp). For object manipulation, however, the motor system frequently has to select a single posture from a multitude of valid solutions. Therefore, a small number of end-state comfort studies also focused on non-binary posture selection. Haggard (1998) measured finger positions in an object rotation task to demonstrate that the initial ad/abduction of the wrist varied as a function of the object's target orientation. Similar results were replicated in a continuous posture selection task by Zhang and Rosenbaum (2008). Both studies were restricted to ad/abduction movements of the wrist. The binary selection of posture used in the majority of end-state comfort experiments, however, resulted from pro/supination movements of the wrist (cf. Rosenbaum, Cohen, Meulenbroek, & Vaughan, 2006). Therefore, the aim of CHAPTER 2 is to determine whether the end-state comfort effect also applies to these pro/supination movements if posture selection is not limited to a binary solution. If the end-state comfort effect was reproduced in a continuous posture selection task, it would support the notion that the previous findings demonstrated in binary tasks also apply to the continuous posture selection that is required in a complex environment. With regard to sequential effects, continuous posture selection until now has not been addressed at all. According to the *plan-modification hypothesis*, sequential effects result from a reuse and modification of a former movement plan (Rosenbaum et al., 2007). The modification is supposed to cause lower cognitive costs than the creation of a new movement plan. In a complex environment, however, the motor system has to select a single posture from a multitude of valid solutions. The cognitive costs for both the creation of a new movement plan and the modification of a former movement plan might therefore differ from those of previously studied, binary tasks (Kelso et al., 1994; Rosenbaum & Jorgensen, 1992; Weigelt et al., 2009). A second aim of Chapter 2 thus is to verify whether sequential effects are still present if posture selection is not limited to a binary solution. To this end, a sequential, perceptual-motor task was created, which offered a continuous range of valid grasp postures for each movement. Participants had to open a column of drawers in a sequential order, grasping each drawer on a cylindrical knob. If sequential effects were present under these continuous conditions, it would provide convincing support that they constitute a general rule for posture selection.

Towards a Cognitive Interpretation of Posture Selection

To date, the question whether sequential effects reflect cognitive features of the movement selection process (Rosenbaum & Jorgensen, 1992) or dynamical features of the mechanical system (Kelso et al., 1994) is still unresolved. In a study on hand path priming (Jax & Rosenbaum, 2007), the authors showed that sequential effects were transferred to the contra lateral arm, which supports their cognitive nature. The cognitive interpretation of sequential effects states that, within a range of indifference, participants are equally content with either grasp type (Rosenbaum & Jorgensen, 1992). A new movement plan can then be created by a modification of the former plan. Thus, sequential effects reduce the cognitive costs of movement planning. So far, sequential effects of posture selection have only been demonstrated in binary studies (Kelso et al., 1994; Rosenbaum & Jorgensen, 1992; Weigelt et al., 2009). In a continuous task space, however, the idea of a binary switch of posture and a restricted range of indifference is no longer viable, as the motor system can continuously adapt the selected posture for each movement trial. Therefore, in Chapter 3, a revised interpretation of sequential effects is proposed, which applies to both continuous and binary posture selection. It is hypothesised that each executed movement is a weighted function of two factors, (1) the anticipated cognitive cost of creating a new movement plan from scratch and (2) the anticipated mechanical cost of executing the given motor task with the previous movement plan. The motor system seeks to optimise the total costs of each executed movement. This optimisation process has two theoretical boundary conditions. If cognitive costs were insignificant, the motor system would only have to minimise the mechanical costs and, thus, create a new, optimal movement plan for each trial. If mechanical costs were insignificant, the motor system would only have to minimise the cognitive costs and, thus, reuse the previous movement plan for each trial. Depending on the relative weight of the cost factors, the optimal solution shifts between these boundary conditions. In a sequential, binary task, this cost optimisation should result in a range of indifference. Within the range of indifference, the anticipated mechanical cost is lower than the anticipated cognitive cost of creating a new movement plan and, thus, the previous grasp type is reused. Once the anticipated mechanical cost of executing the task with the previous movement plan exceeds the anticipated cognitive cost of creating a new movement plan, the grasp type is switched and the range of indifference ends. This behaviour was described in a number of previous studies (Kelso et al., 1994; Rosenbaum & Jorgensen, 1992; Weigelt et al., 2009). In a sequential, non-binary task, the cost optimisation should result in a continuous adaptation of the selected posture.

Sequence-specific differences in posture should be present. The magnitude of the sequential effects should depend on the relative weight of the cost factors. For example, increasing the mechanical cost of the task should change the relative weight of the mechanical cost factor on movement execution and, thus, reduce the magnitude of the sequential effects. The aim of Chapter 3 is to corroborate this cost optimisation hypothesis. To this end, a sequential, continuous posture selection task (opening a column of drawers) was created. A braking mechanism was installed on one of the drawers to increase the mechanical costs of the task. The magnitude of the sequential effects was measured before and after a manipulation phase with increased mechanical costs. If the magnitude of the sequential effects was reduced after the manipulation phase, it would support the cost optimisation hypothesis. The retention of this magnitude change after the end of the manipulation phase would further indicate the formation of a cognitive representation of the increased mechanical costs and, thus, prove the cognitive nature of sequential effects as proposed by Rosenbaum and Jorgensen (1992).

Transfer of Posture Selection Rules to Pointing Movements

In their study on macroscopic effects of manual control (Rosenbaum & Jorgensen, 1992), the authors proposed two fundamental rules for posture selection in aimed limb movements. Whereas the end-state comfort effect demonstrates the anticipation of a subsequent movement state (Rosenbaum et al., 1990), sequential effects indicate the persistence to a previous movement state (Rosenbaum & Jorgensen, 1992). The anticipation of a subsequent movement state and the persistence to a previous movement state have been reproduced in a number of studies (Ansuini et al., 2006; Cohen & Rosenbaum, 2004; Hesse & Deubel, 2010; Kelso et al., 1994; Short & Cauraugh, 1997, 1999; Weigelt et al., 2006, 2009; Zhang & Rosenbaum, 2008). All of these studies were restricted to reaching and grasping tasks. Rules to select a single posture from multiple valid solutions for a target location, however, are a prerequisite for all types of aimed limb movements. Thus, they should also apply to pointing movements. Several characteristics of pointing movements have already been described in the literature: Target location of a pointing movement, for example, is encoded in an external frame of reference (Baud-Bovy & Viviani, 1998; Caminiti, Johnson, Galli, Ferraina, & Burnod, 1991; Kaminski & Gentile, 1989). End-point variance at the target location increases with hand velocity (Crossman & Goodeve, 1983; MacKenzie, Marteniuk, Dugas, Liske, & Eickmeier, 1987; Prablanc, Echallier, Komilis, & Jeannerod, 1979; Schmidt, Zelaznik, Hawkins, Frank, & Quinn Jr, 1979), but only if movements are performed under visual control (Adamovich, Berkinblit, Fookson, & Poizner, 1998, 1999; Adamovich, Berkinblit, Smetanin, Fookson, & Poizner, 1994; Soechting & Flanders, 1989). This result signifies that pointing movements are subject to online corrections based on visual feedback (Keele & Posner, 1968; Woodworth, 1899). The hand path to the target location is explained by the *equilibrium point hypothesis* (Feldman, 1966; Flash, 1987; Hogan, 1984), which states that only the target posture of a movement has to be specified. The motor system sets the corresponding stiffness values for the antagonistic muscles of each joint. Spring-like properties of the muscles then drive the joints towards the point of force equilibrium. Experimental observation indicates that the shift of the stiffness values from an initial posture to the target posture is gradual (Bizzi, Accornero, Chapple, & Hogan, 1982). The equilibrium point hypothesis, however, does not address the problem of how the target posture is selected from a multitude of valid solutions. The aim of Chapter 4 is to verify whether the posture selection rules identified for reaching and grasping movements also apply to pointing movements. For this purpose, a sequential pointing task was created in a virtual and in a physical environment. Participants had to point to a row of targets in the frontal plane in a sequential order. The selected task allowed for the measurement of both anticipation of a subsequent movement state and persistence to a previous movement state. If these effects were reproduced in a pointing task, it would support the hypothesis that the motor system uses the same posture selection rules for different types of aimed limb movements.

Motor Primitives as a Posture Selection Rule

Bernstein (1967) proposed the concept of motor primitives as a solution to the redundancy problem. He suggested that multiple muscles were controlled as a unit by a single motor command, thus reducing the number of independent degrees of freedom of the muscular system. Such muscle synergies were reliably reproduced in a number of studies on vertebrates (d'Avella & Bizzi, 1998, 2005; d'Avella et al., 2006, 2003). Neurophysiological research (Graziano et al., 2005, 2002), however, demonstrated that electrical microstimulation of the primate motor cortex evoked complex final arm postures, independent of the required muscle activity. This implies that the motor cortex is organised on a postural level. Several studies identified postural motor primitives of human arm movements (Berret et al., 2009; Bockemühl et al., 2010; Debicki & Gribble, 2005; Sabatini, 2002; Thomas et al., 2005). In comparison to muscle synergies, postural motor primitives offer a considerable advantage for the planning of aimed limb movements: A single motor transformation is sufficient to map a designated target position in Cartesian space onto a set of motor primitives. To solve the redundancy problem for this transformation, the number of motor primitives has to match the number of degrees of freedom of the target space. That way, each target location can only be reached by one unique combination of the motor primitives. If only one posture is valid for each target location, motor primitives constitute a stand-alone rule for posture selection, which renders additional posture selection rules such as end-state comfort and sequential effects unnecessary. In all previous studies on aimed limb movements, targets were located on two-dimensional planes, but a minimum of three motor primitives was required to capture most of the data variance. This result indicates that motor primitives alone are not sufficient to solve the redundancy problem of posture selection. In Chapter 5, two potential shortcomings of previous studies are addressed: First, in a complex environment, objects can be located anywhere in the three-dimensional workspace of the arm. In order to reach arbitrary locations in this workspace, a minimum of three independent degrees of freedom is required. Thus, it would make no sense for the motor system to use less than three motor primitives for aimed limb movements. The use of two-dimensional target planes is therefore questionable. Second, all mentioned studies on aimed limb movements were restricted to reaching and catching movements. Reaching movements, however, require up to six independent degrees of freedom to translate and rotate the hand to match the position and orientation of the target object. Thus, the number of used motor primitives has to exceed the dimensionality of the target space in order to satisfy the task demands. For motor primitives to serve as a stand-alone rule for posture selection, the task must not require more than three independent degrees of freedom. Pointing movements, in theory, require only three independent degrees of freedom to translate the hand to the target location. Thus, task demands could be satisfied by three motor primitives. In Chapter 5, a pointing task was created in a virtual environment. Participants had to point to virtual targets spaced uniformly in the three-dimensional workspace of the arm. It is hypothesised that three motor primitives capture most of the postural data variance of unrestrained, three-dimensional pointing movements. That way, motor primitives would constitute a stand-alone posture selection rule, which could supersede additional rules such as end-state comfort and sequential effects. This result would further prove that postural motor primitives not only reduce the number of independent degrees of freedom of the motor system, but provide a unique solution to the redundancy problem of posture selection for simple tasks (Bernstein, 1967).

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Motor Control Strategies in a Continuous Task Space

CHAPTER 2

Abstract Previous studies on sequential effects of human grasping behaviour were restricted to binary grasp type selection. We asked whether two established motor control strategies, the end-state comfort effect and the hysteresis effect, would hold for sequential motor tasks with continuous solutions. To this end, participants were tested in a sequential (predictable) and a randomised (non-predictable) perceptual-motor task, which offered a continuous range of posture solutions for each movement trial. Both the end-state comfort effect and the hysteresis effect were reproduced under predictable, continuous conditions, but only the end-state comfort effect was present under non-predictable conditions. Experimental results further revealed a work range restriction effect, which was reproduced for the dominant and the non-dominant hand.

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Introduction

Any reaching movement towards a target located in three-dimensional space requires a series of transformations between sensory and motor coordinate systems. Several of these transformations involve one-to-many mappings, which, in theory, create an infinite number of possible movement kinematics (Jordan & Wolpert, 1999). Experimental observations of reaching movements have demonstrated that, for a reasonably large class of these movements, a number of kinematic parameters tend to remain invariant, independent of movement direction, movement speed, and movement location (Atkeson & Hollerbach, 1985; Flash, 1987; Hogan, 1984). To create such a reproducible behaviour, the central nervous system has to reduce the redundant degrees of freedom that occur from the neural signal to the movement kinematics (Bernstein, 1967).

Optimisation theory provides a computational approach to impose constraints onto the movement selection system (Jordan & Wolpert, 1999). The description of movement kinematics is reduced from time-varying values of joint angles to a single optimality measure that encodes the cost of the movement. One computational model, in which movement selection is based on a cost function for the motor system, as well as on temporal and spatial demands of the task, is the knowledge model by Rosenbaum and colleagues (Rosenbaum, Engelbrecht, Bushe, & Loukopoulos, 1993; Rosenbaum, Loukopoulos, Meulenbroek, Vaughan, & Engelbrecht, 1995). The model claims that the final posture of a movement is created from a set of stored posture representations. Each posture representation is evaluated for its contribution to task demands and a single, target related posture is created as a weighted sum of all posture representations.

Experimental evidence suggests that the motor system assigns a higher priority to the terminal posture of a movement than to the movement itself and utilises posture optimisation as a criterion for movement selection (Marteniuk & Roy, 1972; Rosenbaum, Halloran, & Cohen, 2006; Rosenbaum, Meulenbroek, & Vaughan, 1999). For example, a study by Rosenbaum and colleagues (1990) showed that, when reaching for the same horizontal bar, participants use different initial grasps depending on which end they intend to place on a target disk on the table. By adopting an uncomfortable initial posture (i. e. an underhand grasp), participants avoided ending their movements in an awkward terminal posture. This behaviour was termed the *end-state comfort effect* (Rosenbaum et al., 1990).

The end-state comfort effect has been reliably reproduced in a series of experiments on humans (Cohen & Rosenbaum, 2004; Rosenbaum et al., 1990; Short & Cauraugh, 1997; Weigelt, Cohen, & Rosenbaum, 2007; Weigelt, Kunde, & Prinz, 2006) and other primates (Weiss, Wark, & Rosenbaum, 2007). A number of possible explanations for the end-state comfort effect have been postulated, such as the minimisation of time in awkward postures (Rosenbaum & Jorgensen, 1992), the exploitation of potential energy (Rosenbaum & Jorgensen, 1992), or the precision hypothesis (Rosenbaum, van Heugten, & Caldwell, 1996). The most plausible explanation for end-state comfort in positioning movements (i. e. when placing an object against a target) is provided by the precision hypothesis (Short & Cauraugh, 1997), which states that it is easier to make positioning movements near the middle of the range of motion than near the extremes (Rosenbaum et al., 1996). A number of experiments support the precision hypothesis as a contributing factor behind the end-state comfort effect (Rosenbaum et al., 1996; Rossetti, Meckler, & Prablanc, 1994; Short & Cauraugh, 1999). From a cognitive point of view, it is much simpler to represent and address the terminal posture of a movement than to represent and control the whole movement dynamics, as the distance between the current and the final body posture can be considered the movement itself (Jeannerod, 1996; Rosenbaum, Cohen, Jax, Weiss, & van der Wel, 2007; Schack, 2004).

Many of the findings mentioned above were concerned with discrete motor acts, that is, tasks in which participants were asked to carry out a single object manipulation per trial. In everyday life, tasks are carried out in the context of ongoing sequences of behaviour. So far, only few experiments were conducted on the planning of grasping sequences. The first experiment that dealt with sequential effects in grasping and object manipulation was performed by Rosenbaum and Jorgensen (1992). Participants were asked to grasp a bar that was horizontally supported by a cradle and to place its left or right end against one of 14 targets. The targets were arranged vertically on the shelves of a bookcase and had to be contacted in either ascending or descending order. The experiment demonstrated that ongoing grasp selection (overhand vs. underhand) was influenced by the type of grasp used in the previous trial: When asked to place the right end of the bar against the targets, participants persisted in using an overhand grasp in the descending target condition and an underhand grasp in the ascending target condition. This behaviour of the motor system has later been termed *motor hysteresis* (Kelso, Buchanan, & Murata, 1994); a name originating from the field of physics and characterising any system that exhibits path-dependence of its output signal.

One explanation for such motor hysteresis effects postulates a *range of indifference*, within which participants are equally content in using either an overhand or an underhand grasp (Rosenbaum & Jorgensen, 1992). Therefore, a new movement plan can be generated by small adaptations to the former one, causing less cognitive load than the creation of a movement plan from scratch (Rosenbaum et al., 2007). From a biomechanical point of view, the perseverance of the motor system indicates that, within the range of indifference, the additional cognitive costs of creating or loading an entirely new movement plan exceed the represented energetic costs of remaining in a suboptimal posture. The motor hysteresis effect was reproduced in a number of experiments (Kelso et al., 1994; Weigelt, Rosenbaum, Hülshorst, & Schack, 2009).

A small number of studies focused on the combination of end-state comfort and hysteresis effects (Rosenbaum & Jorgensen, 1992; Short & Cauraugh, 1997; Weigelt et al., 2009). All of them were restricted to the measurement of binary movement features: Participants were forced to decide between an overhand and an underhand grasp when reaching for a bar or opening a drawer. Due to the redundant degrees of freedom of the motor system, however, the terminal posture of a reaching movement in a complex environment usually is derived from a continuum of possible solutions. Thus, the investigation of movements in a continuous task space may have important implications for the further understanding of motor planning.

Hysteresis effects in a continuous task space have already been investigated in a number of studies. Meulenbroek and colleagues (1993) demonstrated a tendency of the motor system to continue using already recruited limb segments in a drawing task. Two studies concerned with hand path priming (Jax & Rosenbaum, 2007; van der Wel, Fleckenstein, Jax, & Rosenbaum, 2007) showed that increased curvature of the hand path persisted for some trials after an obstacle had to be cleared. While this modification of the hand path was inevitably accompanied by a modification of posture, none of the mentioned studies analysed the effects of motor hysteresis in posture space.

The end-state comfort effect has been investigated in non-binary posture space for wrist adduction and abduction. Haggard (1998) employed a discrete measurement of finger positions on an octagonal object to demonstrate that participants changed the orientation of their hand depending on how they planned to move the object. Zhang and Rosenbaum (2008) obtained similar results with an extended experimental setup, using a round object and continuous measurements of hand orientation. The experiment demonstrated that the orientation of the hand varied continuously as a function of the upcoming target position. Both studies were focused on anticipatory effects of subsequent hand postures, but not on sequential effects of previous postures.

However, these effects may have important implications for the further understanding of motor planning. We asked the question of whether or not movement selection criteria like the end-state comfort effect and the motor hysteresis effect would hold for a sequential motor task with continuous solutions. If both effects could be reproduced under these conditions, it would provide convincing support of their general significance for motor planning.

To approach this issue we designed a sequential, perceptual-motor task, which offered a continuous range of posture solutions for each movement trial. Participants were asked to open a column of drawers in a sequential, predictable order, grasping each drawer on a protruding cylindrical knob. The amount of arbitrary hand pro/supination was measured with an optical motion capture system. Thus, the dependent variable is comparable to the original study by Rosenbaum and Jorgensen (1992), in which the binary switch between overhand and underhand grasp was mainly due to pro/supination of the hand. We hypothesised that both the end-state comfort and the hysteresis effect would be reproduced under continuous conditions.

Experiment 1

Participants

Twenty-one students (13 female and 8 male, mean age 23.4 years, age range 21–30 years) from Bielefeld University participated in the experiment. All participants were right handed (by self-report) and had normal mobility of the right hand, arm and upper body. Participants characterised themselves as neurologically healthy and were naïve to the purpose of the study. Before the experiment, each participant provided his or her informed consent and read a detailed set of instructions concerning the required task. The participants did not receive financial compensation for their participation in the study. The study was in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki and approved by the local ethics committee.

Materials

The apparatus used was a tall bookcase (222 cm high, 30 cm wide and 104 cm deep) with nine wooden shelves. The lowest shelf was 92.5 cm from the floor, the highest shelf 192.5 cm, and the distance between adjacent shelves was 12.5 cm. On each shelf, a cardboard drawer (8 cm high, 22 cm wide and 31 cm deep) was placed, with a number from 1 (lowest) to 9 (highest) inscribed on the right side. Between the top side of each drawer and the bottom side of the next shelf a leeway of 3 cm ensured that the drawers could be opened and closed easily. A stop mechanism allowed for a maximum pullout range of 18 cm and a counterweight on the back of the drawer prevented it from tilting. A wooden knob with a diameter of 7 cm and a depth of 4 cm was affixed to the centre of each drawer front. The centre of the lowest knob was at 96.5 cm and the centre of the highest knob at 196.5 cm above the floor. A stack of wooden plates (each 1.5 cm high, 30 cm wide and 104 cm deep) was used to standardise body height of the participants (see next section).

Procedure

Preparation of Participants and Experimental Setup

Each participant was tested individually. Retro reflective markers were attached to three bony landmarks on the wrist and hand via palpation (see table 2.1). Additional reflective materials (e. g. watches, rings) had to be removed by the participant.

To standardise the body height of the participants, a stack of wooden plates was set in front of the bookcase. The plates were arranged parallel to the bookcase, with their right hand side aligned with the left hand side of the bookcase. The number of plates was adjusted to each participant's height, so that the

Table 2.1: Anatomical landmarks, position/direction vectors and segment definition used for the kinematic model of the right and left hand.

Anatomical landmarks		
Code	Description	
RS	*Processus styloideus radii*	
US	*Processus styloideus ulnae*	
MC	*Os metacarpale tertium* (dorsal of the *capitulum*)	
Position and direction vectors		
Code	Description	Computation
WC	centre of the wrist joint	$(RS + US)/2$
$\mathbf{d_1}$	direction vector	$WC - MC$
$\mathbf{d_{2,right}}$	direction vector	$US - RS$
$\mathbf{d_{2,left}}$	direction vector	$RS - US$
CC	centre of the *capitulum*	on a plane normal to $\mathbf{d_1} \times (\mathbf{d_2} \times \mathbf{d_1})$; palmar from MC at a distance of $0.5 \times$ *hand thickn.*+*marker radius*; $(MC - CC)$ and $(WC - CC)$ form right angle
Segment definition		
Code	Description	Computation
$\mathbf{o}$	origin	WC
$\mathbf{x}$	$\mathbf{x}$-axis	$\mathbf{y} \times \mathbf{z}$
$\mathbf{y}$	$\mathbf{y}$-axis	$CC - WC$
$\mathbf{z}$	$\mathbf{z}$-axis	$\mathbf{d_2} \times \mathbf{y}$

shoulder height (palpated at the acromion) was aligned with the centre of drawer #6 (see figure 2.1).

The participant positioned him/herself on the stack of wooden plates in front of and slightly to the left of the bookcase, at a

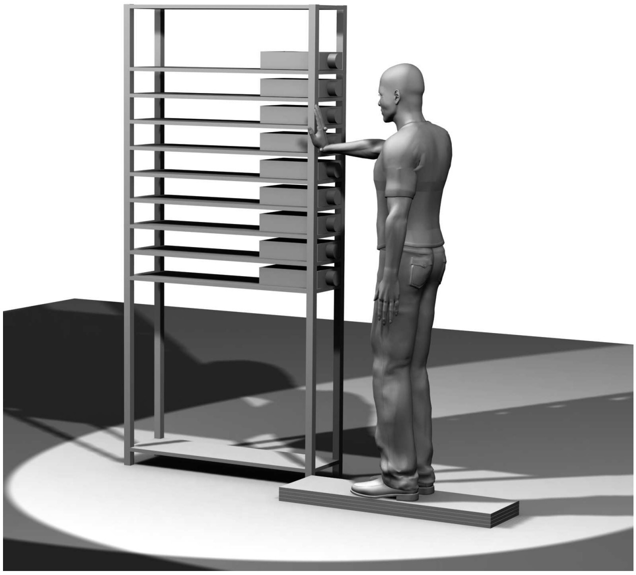

Figure 2.1: Schematic of the experimental setup. The participant is positioned on a stack of wooden plates (shoulder height aligned with drawer #6) in front and 30 cm to the left of the bookcase. The right arm is stretched straight ahead, with the heel of the hand touching the front of the drawers.

distance of approximately 90 cm from the front of the drawers. Each participant then stretched his/her right arm straight ahead, with the palm pointing towards the bookcase and the fingers pointing upwards. He/she then moved forward until the heel of the hand touched the front of the drawers (see figure 2.1). This way, the distance to the bookshelf was normalised to the different arm lengths of the participants.

Task Execution

Each participant had to open and close the drawers in ascending and descending sequences of trials, the order of which was counterbalanced across participants. Participants started each trial from an initial position, with the right arm hanging loosely on the side of the body and the palm of the hand touching the thigh. On a signal from the experimenter, the participant (1) raised the arm to the first drawer, (2) closed the fingers around the knob, (3) opened the drawer to the full extent, (4) closed the drawer and (5) returned the arm to the initial position. This sequence was repeated for each drawer until all drawers had been attended to. After a short break of approximately 30 s, the participant started with the second sequence of trials.
The entire experiment lasted approximately 30 min.

Motion Capture

Movement data were recorded using an optical motion capture system (Vicon Motion Systems, Oxford, UK) consisting of six MX-3+ CCD cameras with 50 Hz temporal and approximately 0.5 mm spatial resolution. Three spherical retro reflective markers (diameter 14 mm) were used to measure the position of the anatomical landmarks (see table 2.1) on the hand and wrist. Cartesian coordinates of the markers were calculated from the camera data via triangulation. No filtering of the raw data was done. Marker trajectories were manually labelled in Vicon Nexus 1.1 and exported to Vicon Bodybuilder for post processing.

Kinematic Model

For the kinematic analysis, the hand was modelled as a single, rigid segment (see table 2.1). Markers were attached to the radial (RS) and ulnar styloid (US) and to the third metacarpal (MC), on the dorsal side of the *capitulum*. The wrist joint centre (WC)

was calculated halfway between RS and US (see table 2.1). Two direction vectors were calculated, one pointing from the third metacarpal to the wrist joint centre ($\mathbf{d_1} = WC - MC$) and a second one passing through the wrist ($\mathbf{d_2} = US - RS$). The *capitulum* centre (CC) was then defined on a plane normal to $\mathbf{d_1} \times (\mathbf{d_2} \times \mathbf{d_1})$. It was positioned palmar from MC at a distance of $0.5 \times hand\ thickness + marker\ radius$ in a way that $MC - CC$ and $WC - CC$ formed a right angle.

A local hand coordinate system was defined. The origin was set at the wrist joint centre (WC). The **y**-axis was defined by the wrist joint centre and the *capitulum* centre, pointing towards the *capitulum* ($CC - WC$). The **z**-axis was defined by the cross product of the wrist axis, pointing from radius to ulna, and the **y**-axis ($\mathbf{d_2} \times \mathbf{y}$). The **x**-axis was defined as the cross product of the **y**- and the **z**-axis ($\mathbf{y} \times \mathbf{z}$), in order to create a right handed coordinate system.

Pro/supination angles were calculated as a transformation of the laboratory's coordinate system into the local hand coordinate system. The rotations were conducted in the sequence $z \mapsto x' \mapsto y''$ around floating axes. The laboratory's coordinate system was defined with the **z**-axis pointing upwards and the **x**- and **y**-axis parallel to the floor. That way, the rotational axis for the pro/supination movement was aligned with the **y**-axis of the hand and the pro/supination angle was zero when the hand was parallel to the floor in a palm-downward position. Pronation of the hand caused a decrease of the pro/supination angle, supination caused an increase.

Data Analysis

The longitudinal axis of the bookcase was aligned on a ray facing towards the origin of the laboratory's coordinate system (i. e. the artificially defined zero point of the three Cartesian axes, located near the centre of the laboratory at ground level). The front of the bookcase was positioned at a distance of approximately 2.3 m from the origin. For the extraction of the pro/supination angle values of the initial grasp, the distance between the centre of the *capitulum* (CC) and the origin of the laboratory's coordinate system was calculated in the **x-y**-plane. To allow for an automatic detection of the distance maxima, a moving average with a width of five frames was applied to the distance graph (see figure 2.2, top panel).

For each drawer, the distance graph started at a low initial value, steeply ascended towards a local maximum and then slowly descended towards a local minimum. The low initial value corresponded to the initial posture of the participant, with the hand positioned next to the thigh. The steep ascent represented the reaching movement towards the drawer, with the local maximum marking the moment when the fingers closed around the knob. The following descent corresponded to the opening of the drawer. The pro/supination angle of the hand was measured at the moment the participant grasped the drawer knob, determined by the position of the first local maximum (see figure 2.2).

For each of the 21 participants, 18 pro/supination angle values of the hand were measured. Of these 18 values, nine belonged to the ascending sequence of trials and nine belonged to the descending sequence of trials. The measurement values of all participants were included into the analysis.

Results

To examine the pro/supination of the hand, we conducted a 2 (sequence: ascending vs. descending) $\times$ 9 (drawer: lowest to highest) repeated measures analysis of variance (ANOVA) on the pro/supination angles. Where appropriate, the Greenhouse-Geisser correction was applied to the p-values; degrees of freedom, however, are reported uncorrected. The main effect of sequence was significant, $F(1, 20) = 11.825, p < .01$. Participants used a more supinated grasp in the ascending sequence of trials than in the descending sequence of trials. The main effect of drawer was also significant, $F(8, 160) = 28.076, p < .001$. Participants used a more supinated grasp for the lower drawers and

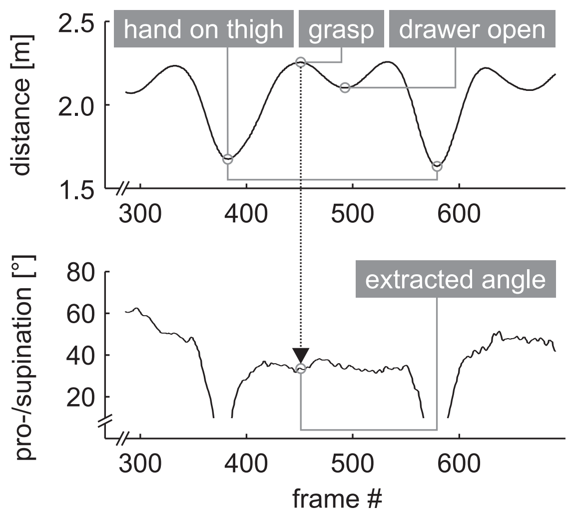

Figure 2.2: Extraction of the pro/supination angle at the moment of initial grasp: top panel: distance between the centre of the *capitulum* and the origin of the laboratory's coordinate system in the **x**-**y**-plane; bottom panel: pro/supination angle; the pro/supination angle is measured in the frame corresponding to the first local maximum of the distance graph.

a more pronated grasp for the higher drawers (see figure 2.3). The interaction of sequence × drawer was not significant.

To examine the overall range of pro/supination angles used by the participants for the ascending and the descending sequence of trials, the difference between the maximum angle value (at or near drawer #1) and the minimum angle value (at or near drawer #9) for each participant and movement direction was calculated. Pro/supination angle ranges for the ascending sequence of trials varied from 13.3° to 162.3°, for the descending sequence of trials from 5.9° to 161.3°. The correlation between the angle ranges of the ascending and the descending sequence of trials was significant (see figure 2.4, $r^2 = 0.68, p < .01$), which

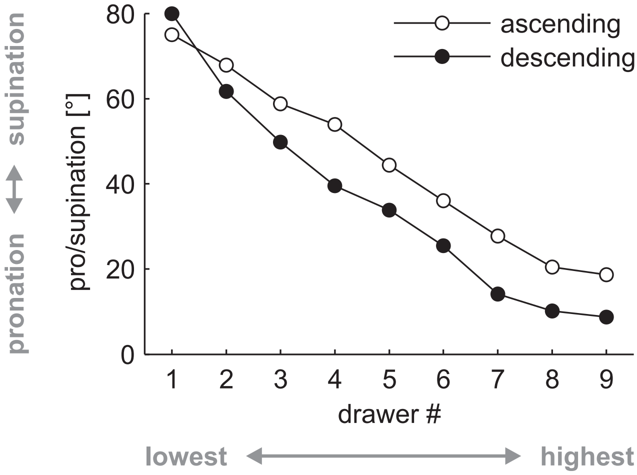

Figure 2.3: Pro/supination angle for the ascending and the descending sequence of trials. Each data point represents the mean value of all 21 participants for each drawer and movement direction, respectively.

shows that participants used similar ranges for the ascending and descending sequence of trials.

Discussion

In the first experiment, we introduced a sequential, perceptual-motor task, which offered a continuous range of posture solutions for each movement trial. Participants were asked to open a column of drawers in a sequential order, grasping each drawer on a protruding cylindrical knob. The pro/supination angle of the terminal posture participants adopted at each drawer height was measured with an optical motion capture system.

It was predicted that participants would continuously modify the pro/supination angle for successive drawers to ensure a comfortable terminal posture for each drawer height. The results of the experiment confirmed this hypothesis. Higher drawers were opened with a more pronated grasp, whereas lower drawers were

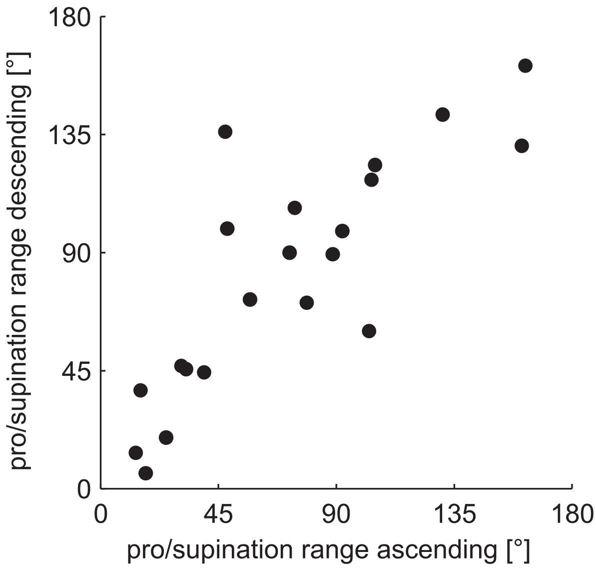

Figure 2.4: Correlation plot of the pro/supination angle ranges for the ascending and the descending sequence of trials. Each data point represents one participant (single measurement). Pro/supination angle ranges show a significant correlation ($r^2 = 0.68, p < .01$).

opened with a more supinated grasp. The pronation of the hand increased continuously during the ascending sequence of trials and decreased continuously during the descending sequence of trials. This result indicates that the motor system utilises end-state comfort as a planning criterion for tasks with continuous solutions.

Furthermore, we expected motor hysteresis effects to occur between ascending and descending sequences of trials. From an end-state comfort point of view, participants were, in principle, able to assume an optimal posture for each drawer. Due to the additional cognitive costs that arise when one has to plan an optimal posture from scratch, however, we assumed the actual terminal posture to be created by modifications to the most recent posture, representing a trade-off between cognitive and biomechanical costs. The experimental results confirmed this assumption. Participants used a more supinated grasp for the ascending sequence of trials and a more pronated grasp for the descending sequence of trials, indicating perseverance to previous grasps and, thus, motor hysteresis.

Additional data analysis revealed that the fraction of the pro/supination range that was actually utilised to satisfy the end-state comfort criterion varied considerably (by factor 10) across different participants. This implies that a majority of the participants was not even near the extreme points of the anatomically feasible work range of the wrist joint, a finding that is further supported by the fact that the mean pro/supination value for the bottom drawer was considerably lower than the maximum supination angle that was anatomically feasible (Boone & Azen, 1979). Both results indicate that this *range restriction effect* does not occur due to anatomical constraints. Although the fraction of the work range used varied considerably between different participants, the experimental results revealed a strong correlation of pro/supination ranges between ascending and descending movement sequences. If participants only used a small fraction of the whole work range in the ascending sequence of trials, they did the same for the descending sequence of trials. And similarly, if they used a large work range in the ascending sequence of trials, they also used a large work range in the descending sequence of trials.

Experiment 2

The second experiment was conducted to further investigate the generality of two motor control effects: The end-state comfort effect for continuous movements and the restriction of the anatomically feasible range of motion that was found in the first experiment. We approached this issue by verifying whether both effects would be transferred from the dominant to the non-dominant hand and from a sequential order to a random order task, supporting their significance for the motor system. Participants were tested under two counterbalanced conditions: opening the drawers in a pseudo-random order with the dominant hand or the non-dominant hand. Each experimental condition was repeated five times.

Based on the results of the first experiment, it was predicted that participants would use different pro/supination angles for different drawer heights, to satisfy the end-state comfort criterion. In addition, we predicted considerably different fractions of the anatomically feasible work range of the wrist to be used between participants, but similar fractions to be used for the dominant and the non-dominant hand within one participant. Regarding the effect of repetition, we considered an optimisation effect to take place, increasing the used fraction of the feasible range of motion and, by that, the achieved end-state comfort. Based on the hypothesis that the maintenance and modification of a motor plan is an active process and, thus, associated with cognitive costs, we expected the hysteresis effect to be absent in the non-predictable trial sequences of the second experiment.

Participants

Fifteen students (9 female and 6 male, mean age 23.6 years, age range 21–26 years) from Bielefeld University participated in the experiment. Data from one female participant had to be excluded from the data analysis due to a malfunctioning of the recording device. From the remaining participants, thirteen were right handed and one was left handed (by self-report). All participants had normal mobility of their right and left hands, arms, and their upper body. None of the participants had taken part in Experiment 1. All participants characterised themselves as neurologically healthy and were naïve to the purpose of the study. Before the experiment, each participant provided his or her informed consent and read a detailed set of instructions concerning the required task. The participants did not receive financial compensation for their participation in the study. The study was in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki and approved by the local ethics committee.

Materials and Procedure

The same bookcase and drawer setup was used as in Experiment 1. Each participant was tested individually. Retro reflective markers were attached to bony landmarks of both wrists and hands via palpation (see table 2.1).

To standardise the body height of the participants, a stack of wooden plates was set in front of the bookcase. The plates were arranged in parallel to the bookcase, either with their right hand side aligned with the left hand side of the bookcase (for reaching movements with the right arm) or with their left hand side aligned with the right hand side of the bookcase (for reaching movements with the left arm). The position was adjusted by the experimenter between sequences of trials.

Each participant had to open and close the drawers with the dominant hand and the non-dominant hand in five sequences of trials, respectively. The order of hand was counterbalanced across participants. A list of pseudo-random permutations of the drawers, based on the Mersenne twister algorithm (Matsumoto & Nishimura, 1998), was created before the experiment. Referring to this list, the experimenter announced each drawer to the participant. Movement execution was identical to Experiment 1 and had to be repeated for each drawer. Each sequence of trials was followed by a short pause of approximately 30 s.
The entire experiment lasted approximately 30 min.

Motion Capture, Kinematic Model, and Data Analysis

The motion capture procedure was similar to Experiment 1. For the analysis of the right hand, the kinematic model of Experiment 1 was reapplied. To render the kinematic model for the left hand comparable, the direction vector through the wrist ($\mathbf{d_2}$) was inverted, pointing towards the thumb instead of the little finger (see table 2.1). All remaining calculations and segment definitions stayed the same. That way, when both hands were stretched out in front of the participant in a palm-downward position, the orientations of both hand coordinate systems were identical.

Rotations for both hands were calculated similar to Experiment 1. To render the movements of both hands comparable we inverted the sign of the pro/supination angles for the left hand. Thus, for each hand, pronation resulted in a decrease and supination in an increase of the pro/supination angle.

For the data analysis, the pro/supination angles of the hands were measured at the moment the participant grasped the drawer knob (the same definition of 'grasp' was used as in the first experiment). For each of the 14 participants, a total of 90 pro/supination angle values of the hand were measured, corresponding to 9 (number of drawers) $\times$ 5 (number of measurements per drawer) $\times$ 2 (dominant/non-dominant hand) conditions.

Results

To examine the pro/supination of the hand, we conducted a 2 (hand: dominant vs. non-dominant) $\times$ 9 (drawer: lowest to highest) $\times$ 5 (repetitions) repeated measures analysis of variance (ANOVA) on the pro/supination angles. Where appropriate, the Greenhouse-Geisser correction was applied to the p-values; degrees of freedom, however, are reported uncorrected. The main effect of drawer was significant, $F(8, 104) = 24.284, p < .001$, showing that participants used a larger pro/supination angle, i. e. a more supinated grasp, for the lower drawers (see figure 2.5). The main effect of hand was not significant, $F(1, 13) = 0.011, p = .65$. There was no difference in the pro/supination angle between the dominant and the non-dominant hand. The main effect of repetition was also not significant, $F(4, 52) = 1.178, p = .33$, indicating that no adjustment of grasp angles occurred as a function of trial sequence repetition. None of the interactions were significant.

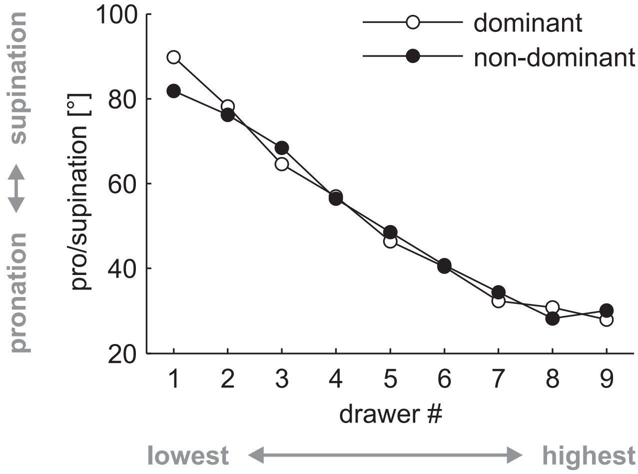

Figure 2.5: Pro/supination angle for the dominant and the non-dominant hand. Each data point represents the mean value of all 14 participants for each drawer and hand, respectively.

To examine the overall pro/supination angle range used by the participants for the dominant and the non-dominant hand, the mean difference between the maximum angle value (at or near drawer #1) and the minimum angle value (at or near drawer #9) for each participant and hand was measured. Mean angle ranges for the dominant hand varied from 25.7° to 126.8° and for the non-dominant hand from 31.4° to 135.7°. The correlation between the angle ranges of the dominant and the non-dominant hand was significant (see figure 2.6 c, $r^2 = 0.67, p < .001$). Participants used similar ranges for the dominant and non-dominant sequences of trials. To examine the effect of participant size on the angle ranges, a correlation analysis between body height and angle range was performed. The correlation for neither the dominant (see figure 2.6 a, $r^2 = 0.08, p = .34$) nor the non-dominant (see figure 2.6 b, $r^2 = 0.07, p = .38$) hand was significant. Hence, participant size did not affect the angle range.

To test for potential hysteresis effects within the randomised sequences, grasp angles for each drawer were classified depending on whether the previously grasped drawer (N–1) was above or below. Accordingly, paired t-tests (N–1 above vs. N–1 below) were conducted for each of the drawers 2–8, which accounted for the high inter subject variance in grasp angle: Only the data of those participants were included that had grasped the respective drawer at least once coming from above and once coming from below. For each selected participant, the mean pro/supination angle of all ascending (N–1 below) and of all descending (N–1 above) trial pairs was calculated. Paired t-tests conducted for each drawer revealed no significant differences in grasping behaviour (all $p > .05$), irrespective of whether the previously grasped drawer (N–1) was above or below. This was similar for the dominant (see figure 2.7) and the non-dominant hand.

Discussion

The main focus of the second experiment was to confirm the generality of two motor control effects: The end-state comfort effect for continuous movements and the work range restriction effect found in the first experiment. It was hypothesised that both effects would be reproduced in a random order task, as well as in the non-dominant hand. Participants were tested under two conditions: opening the drawers in a pseudo-random order with the dominant hand or the non-dominant hand.

The pattern of results confirmed our hypotheses. Participants used a more pronated grasp for the higher drawers and a more supinated grasp for the lower drawers. This behaviour is in line with the end-state comfort criterion. The effect was similarly present for the dominant hand and the non-dominant hand.

The experimental results for the range of motion showed a large variance over all participants, but a significant correlation between the ranges of motion of the dominant and non-dominant

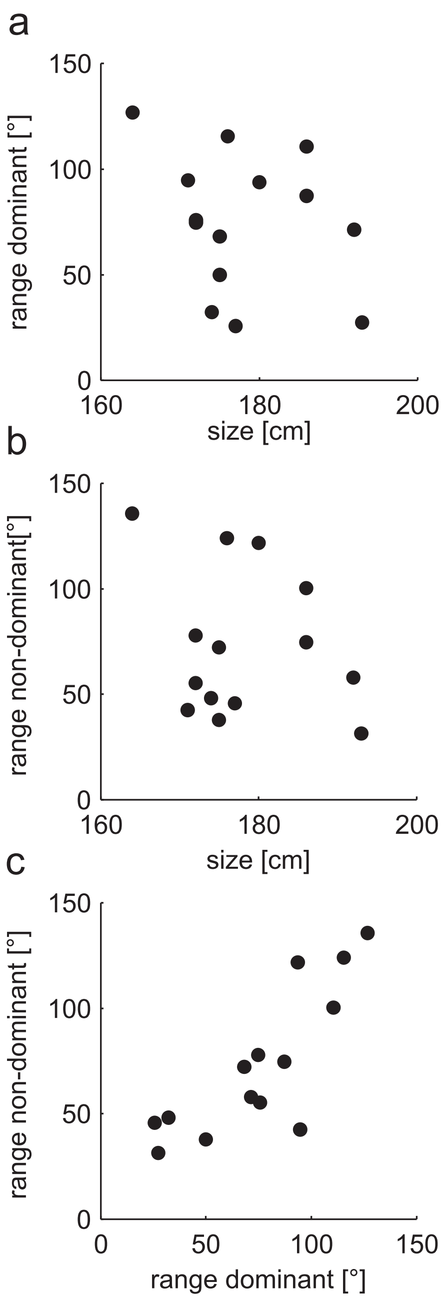

Figure 2.6: Correlation plots; each data point represents one participant (mean of five repetitions); (a) correlation of the pro/supination angle ranges and body height for the dominant hand ($r^2 = 0.08, p = .34$); (b) correlation of the pro/supination angle ranges and body height for the non-dominant hand ($r^2 = 0.07, p = .38$); (c) correlation of the pro/supination angle ranges of the dominant and the non-dominant hand ($r^2 = 0.67, p < .001$).

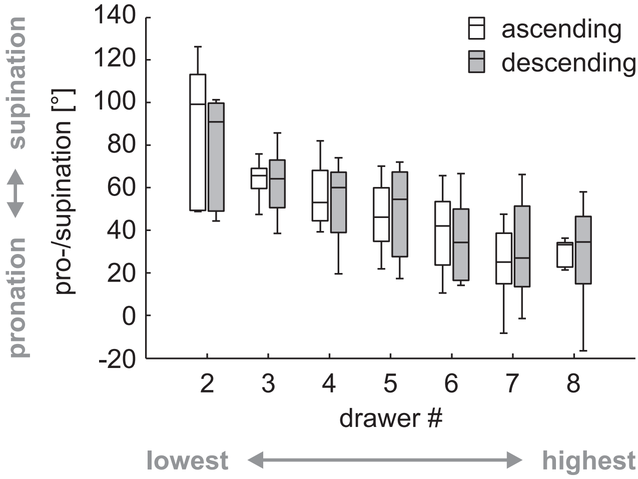

Figure 2.7: Box plot of the pro/supination angle of the dominant hand for the ascending (drawer N–1 below) and descending (drawer N–1 above) condition. Size and composition of the participant subset matching the analysis requirement varies for each drawer. Similar results are found for the non-dominant hand.

hand. This confirms the predictions concerning the work range restriction effect. In addition, no correlation between body size, which also serves as a predictor for the arm length of the participants (Jarzem & Gledhill, 1993), and the range of motion was found. These findings are in opposition to the notion of mechanical constraints of the motor system being the sole cause for the restriction of the feasible work range. Rather, it implies that the restriction of the range of motion found in a majority of participants occurs due to cognitive constraints, which may affect the generation of motor plans and/or the selection of the appropriate motor actions for the sequential task.

We also considered an effect of repetition to occur, as participants could increase the range of motion to increase the amount of end-state comfort over successive sequences of trials. The results, however, revealed no effect of repetition: Participants did not change the utilised pro/supination angle over successive sequences of trials. A possible explanation for the lack of such an optimisation might be that, even with a considerably smaller range of motion than feasible, participants have already reached their individual optimum of end-state comfort and are able to sufficiently plan their actions on the first sequence of trials.

Regarding the hysteresis effect, it was hypothesised that ongoing grasp selection in a non-predictable sequence of trials would not be influenced by the previous trial. The pattern of results confirmed this hypothesis. Hand pro/supination angle for each trial did not depend on the previous trial. A possible explanation for the absence of the hysteresis effect might be that the maintenance and modification of a motor plan in memory is associated with cognitive costs. Therefore, if the probability that the stored motor plan can actually be reused for the upcoming trial decreases due to the unpredictable sequence of trials, the hysteresis strategy might become inefficient.

General Discussion

In the present study, we investigated whether two established motor planning criteria, the end-state comfort effect and the hysteresis effect, would hold for sequential motor tasks with continuous solutions. To this end, we designed a perceptual-motor task, which offered a continuous range of posture solutions for each movement trial. In two experiments, participants were asked to execute predictable and non-predictable sequences of trials. Both the end-state comfort effect and the hysteresis effect were reproduced under continuous, predictable conditions in Experiment 1, but only the end-state comfort effect was present under non-predictable conditions in Experiment 2. Results further revealed a restricted range of motion for the wrist joint, which was reproduced both for the dominant and the non-dominant hand.

The end-state comfort criterion (Rosenbaum et al., 1990) predicts that people plan their movements in a way that ensures a comfortable terminal posture. End-state comfort has been reliably reproduced in a series of experiments investigating binary features of a movement (e. g. overhand vs. underhand grasp; Cohen & Rosenbaum, 2004; Short & Cauraugh, 1997; Weigelt et al., 2007, 2006). End-state comfort in a non-binary posture space was first shown by Haggard (1998) and later reproduced in a continuous posture space by Zhang and Rosenbaum (2008). Both studies demonstrated that the adduction and abduction of the wrist varied as a function of the upcoming target. The present study extends the existing results to pro/supination movements of the hand. Thus, the dependent variable is comparable to the original study by Rosenbaum and Jorgensen (1992), in which the binary switch between overhand and underhand grasp was mainly due to pro/supination of the wrist. We hypothesised that the end-state comfort effect would be reproduced in a continuous posture space. The results of the first experiment confirmed this hypothesis, as participants continuously adopted their posture to satisfy the end-state comfort criterion. These findings extend the original results to a continuous posture space and are consistent with previous studies on hand orientation. By employing an everyday task such as opening a set of drawers, the current study provides empirical evidence of high ecological validity.

In the second experiment, we compared the pro/supination angles of the terminal posture for the dominant and the non-dominant hand. Experimental evidence from early studies suggests differences in movement planning for the left and right hand (Annett, Annett, Hudson, & Turner, 1979). With regard to bimanual tasks, ambivalent results have been produced so far. Weigelt and colleagues (2006) found no hand specific differences of the terminal posture for discrete, goal directed movements. Participants minimised awkwardness of both hands at the end of the bimanual object manipulation, even when different grips and motor commands were required. Using more complex task conditions, however, Janssen and colleagues (Janssen, Beuting, Meulenbroek, & Steenbergen, 2009; Janssen, Crajé, Weigelt, & Steenbergen, 2009) demonstrated differences in the preference of end-state comfort between the two hands. For unimanual tasks, differences between the left and the right hand were demonstrated for movement initiation time (Carson, Chua, Goodman, Byblow, & Elliott, 1995). Participants that were provided with unspecific information concerning the position of the movement target exhibited a left hand advantage for speed of initiation. Furthermore, Rosenbaum and colleagues (1996) showed that participants exhibited a movement time advantage for the right hand in a forearm rotation task. Hughes and Franz (2008), on the other hand, found no differences in movement initiation time between both hands, as well as no differences in terminal posture for a unimanual, binary grasp selection task. To our knowledge, no comparison of the left and right hand for the terminal posture in a continuous task space has been done so far. The second experiment did not reveal any differences between the terminal postures of the dominant and the non-dominant hand. The present study shows similarities of the continuous pro/supination angles instead of binary grasp probabilities and, thus, contributes valuable information to the existing literature on the topic of hand dominance and motor performance.

A second movement planning criterion of the motor system is the motor hysteresis effect (Rosenbaum & Jorgensen, 1992). The motor hysteresis criterion predicts that, in a sequential motor task, people persist in the type of movement used before. Several experiments corroborate this prediction (Kelso et al., 1994; Weigelt et al., 2009). Rosenbaum and colleagues (2007) interpreted motor hysteresis as a way to reduce the cognitive costs associated with the creation of a new movement plan. A limitation of previous experiments was the enforcement of binary grasp types. Because of this limitation, the cognitive costs for this binary switch of the grasp type might have been increased and, as a result, the importance of motor hysteresis as a movement planning criterion might have been overestimated. Hysteresis effects in a continuous task space were analysed in studies on hand path priming (Jax & Rosenbaum, 2007; van der Wel et al., 2007). Both studies employed the continuous measurement of hand path curvature to demonstrate sequential effects of the end-effector trajectory after clearing an obstacle. Though this modification of the end-effector trajectory was inevitably accompanied by a modification of posture, none of the studies focused on hysteresis effects in posture space. With the drawer opening task used in the present study, hysteresis effects in a continuous posture space could be demonstrated without modifications of the end-effector position (same drawer height). Referring to the original interpretation by Rosenbaum and colleagues (2007), we predicted the motor hysteresis effect to be reproduced in continuous posture space, even though no binary switch was required between successive trials. The results of the first experiment confirmed this prediction, as the pattern of pro/supination angles revealed sequence-dependent grasping behaviour. The present study extends the previous results on posture hysteresis (Rosenbaum & Jorgensen, 1992; Weigelt et al., 2009) by providing continuous measurements of pro/supination angle distributions. It thus yields further statistical support of the motor hysteresis effect and highlights the importance of motor hysteresis as a criterion for motor planning.

To compare hysteresis effects between the sequential (predictable) task of the first experiment and the randomised (non-predictable) task of the second experiment, the data of the randomised experiment were analysed for effects of the previous trial. Based on the hypothesis that the maintenance and modification of a motor plan is an active process and, thus, associated with cognitive costs, we expected the hysteresis effect to be absent in the non-predictable trial sequences of the second experiment. The results confirmed this prediction. The grasp angle participants used in each trial did not depend on the grasp angle used in the previous trial. This result is in contrast to a previous study on hand path priming by Jax and Rosenbaum

(2007), demonstrating hysteresis effects for both predictable and non-predictable sequences of trials. The contrasting result can be explained by the differences of the experimental designs: In the study by Jax and Rosenbaum, maintenance of the original motor plan resulted in a successful (yet less efficient) movement in 100 % of the cases. In the present study, maintenance of the original motor plan only resulted in a successful movement in about 25 % of all cases. Thus, if the cognitive costs for the maintenance and modification of a motor plan is weighted with the low probability that the motor plan can actually be reused, the hysteresis strategy may become inefficient for the motor system. Therefore, our results are consistent with the previous results (Jax & Rosenbaum, 2007; Weigelt et al., 2009) as well as with the original interpretation of the hysteresis effect by Rosenbaum and colleagues (2007). However, a systematic manipulation of the likelihood of using a previous motor plan should be the focus of further studies.

An unanticipated result of the first experiment was the fact that (1) the fraction of the pro/supination range that was actually utilised varied considerably (by factor 10) across different participants and that (2) the mean pro/supination value encountered for the bottom drawer was considerably lower than the maximum supination angle that was anatomically feasible (Boone & Azen, 1979). This indicated that a majority of the participants did not use the full extent of their feasible work range to satisfy the end-state comfort criterion. To our knowledge, this individual restriction of the range of motion has not been described in the literature before.

Based on the assumption that this work range restriction effect was due to cognitive constraints and not due to mechanical constraints of the motor system, we predicted the effect to be present when performing with the contra lateral arm, and in a random order task, respectively. This prediction was confirmed by the results of the second experiment. Participants exhibited similar ranges of motion for the dominant and the non-dominant hand, while the variance of the ranges of motion was large across participants. Furthermore, no correlation between body size and the range of motion was found, supporting the argument that the range restriction effect is indeed due to cognitive constraints of the motor system and not due to mechanical factors.

The cognitive constraints may result from the implicit inclusion of anticipated posture comfort and energetic costs into the generation of motor plans and/or the selection of motor actions (Rosenbaum et al., 1993, 1995). Individual differences in the anticipation and perception of these motor effects, due to previous movement experience or the range of motion participants use in their everyday life tasks, may then create the high inter subject variance. These differences may even result in an individual movement style, similar to a personality trait, that is influenced by different movement cultures experienced in the family and in the workplace. As an alternative explanation, the inter subject variance may also result from other internal factors such as self-regulation and personality traits[1]. Differentiating between those internal factors, however, was not the goal of the current study.

In sum, our findings confirm the generality of the end-state comfort effect and the motor hysteresis effect as important criteria for the planning of movements within sequential tasks with continuous posture solutions. Results further support the hypothesis of motor hysteresis being a trade-off between cognitive and biomechanical costs of a movement and demonstrate a non-biomechanical restriction of the range of motion used to satisfy the end-state comfort criterion.

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Influence of Mechanical Load on Sequential Effects

CHAPTER 3

Abstract Almost two decades ago sequential effects of human grasping behaviour were described for the first time. In a sequential task, participants persisted in using the previous grasp type. According to the plan-modification hypothesis, such sequential effects reduce the movement planning costs and occur within a limited range of indifference. We asked whether the anticipated mechanical costs of a movement would counteract the movement planning costs and, thus, reduce the magnitude of the sequential effect. To this end, participants were tested in a sequential, perceptual-motor task (opening a column of drawers), which offered a continuous range of posture solutions for each trial. In a pre-post-test design, the magnitude of the sequential effect was measured before and after a manipulation phase with increased mechanical costs. Participants displayed a sequential effect for the majority of drawers in the pre-test, which was significantly reduced in the post-test. This finding indicates that each executed movement is a weighted function of both its cognitive and mechanical costs. The result also implies that sequential effects do not result solely from dynamical properties of the motor system, but instead reflect computational features of the movement selection process.

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Introduction

Almost two decades ago Rosenbaum and Jorgensen (1992) published their influential study on macroscopic aspects of manual control. In the first of two experiments, the authors showed that participants used awkward initial grasp postures in order to ensure a comfortable posture at the end of the movement. This *end-state comfort effect* (Rosenbaum et al., 1990) has been reliably reproduced in a number of experiments on humans (see Rosenbaum, Cohen, Meulenbroek, & Vaughan, 2006 for an overview) and other primates (Chapman, Weiss, & Rosenbaum, 2010; Weiss, Wark, & Rosenbaum, 2007). End-state comfort is found both under unimanual (Seegelke, Hughes, & Schack, 2011; Weigelt, Cohen, & Rosenbaum, 2007) and bimanual (Hughes, Reißig, & Seegelke, 2011; van der Wel & Rosenbaum, 2010; Weigelt, Kunde, & Prinz, 2006) task conditions. Sensitivity to end-state comfort has been shown to develop over the lifespan (Stöckel, Hughes, & Schack, 2011; Thibaut & Toussaint, 2010; Weigelt & Schack, 2010). Several possible explanations for the end-state comfort effect have been postulated, such as the minimisation of time in awkward postures (Rosenbaum & Jorgensen, 1992), the exploitation of potential energy (Rosenbaum & Jorgensen, 1992), or the precision hypothesis, which states that it is easier to make positioning movements well within the range of motion than near the extremes (Rosenbaum, Halloran, & Cohen, 2006). Several studies' findings support the precision hypothesis as a contributing factor to end-state comfort sensitivity (Rosenbaum, Halloran, & Cohen, 2006; Rossetti, Meckler, & Prablanc, 1994; Short & Cauraugh, 1997, 1999; Thibaut & Toussaint, 2010).

The robust demonstrations of the end-state comfort effect provide evidence that subsequent postures are anticipated and planned for in advance. This notion is further supported by a number of studies from the field of prehension (Ansuini, Santello, Massaccesi, & Castiello, 2006; Gentilucci, Negrotti, & Gangitano, 1997; Hesse & Deubel, 2010; Marteniuk, MacKenzie, Jeannerod, Athenes, & Dugas, 1987). In an early study from Marteniuk and colleagues (1987), for example, it was shown that the initial reach-to-grasp velocity varied depending on whether the grasped object later had to be thrown or placed. Ansuini and colleagues (2006) further demonstrated that the shape of the hand and the finger positions on a grasped object differed depending on the subsequent precision demands of the task. In a recent paper, Hesse and Deubel (2010) showed that the hand orientation chosen in early movement segments depended on the hand orientation at the end of the movement sequence.

In the second experiment of their original publication, Rosenbaum and Jorgensen (1992) further demonstrated that, in a sequential task, the movements participants selected were not only influenced by the anticipated subsequent movements, but also by the movements they had recently performed: Participants had to grasp a bar and place its left or right end against one of 14 vertically aligned targets in a sequential order. The experiment showed that, for a range of targets, participants persisted in using the previous grasp type (overhand vs. underhand). These *sequential effects* occurred within a *range of indifference*, where participants were equally content with either grasp type. In their *plan-modification hypothesis*, Rosenbaum and colleagues (2007) state that, within the range of indifference, a new movement plan can be created by modifications of the former plan, thus reducing the cognitive costs associated with the creation of a new movement plan from scratch. In aimed limb movements, these cognitive costs result from a series of sensorimotor transformations, which are required to map the designated hand position to a set of appropriate muscle activations that create the movement (Jordan & Wolpert, 1999). A number of these transformations offer multiple solutions. For example, a target position can be reached by different trajectories, and positions along the trajectory can be achieved by different postures. Selection of a single solution therefore requires the motor system to implement and evaluate additional constraints. One may speculate that both end-state comfort and sequential effects are constraints used to select the final posture of a movement.

In contrast to the end-state comfort effect, sequential effects have only been reproduced in a limited number of studies. Meulenbroek and colleagues (1993) demonstrated that participants persisted in using previously recruited limb segments in a drawing task. Studies on hand path priming (Jax & Rosenbaum, 2007; van der Wel, Fleckenstein, Jax, & Rosenbaum, 2007) showed that increased curvature of hand trajectories persisted for several cycles after an obstacle had to be cleared. Diedrichsen and colleagues (2010) demonstrated that passive guidance of the hand along a task-redundant dimension induced a lasting modification of the hand trajectory. Although this modification of the hand trajectory was inevitably accompanied by a modification of posture, none of the mentioned studies focused on sequential effects in posture space. In several studies on humans (Kelso, Buchanan, & Murata, 1994; Rosenbaum & Jorgensen, 1992; Weigelt, Rosenbaum, Hülshorst, & Schack, 2009) and other primates (Weiss & Wark, 2009), such sequential effects of posture selection were demonstrated for identical end-effector positions. In a study by Weigelt and colleagues (2009), for example, participants were asked to open a column of slotted drawers in a sequential order. Results showed that participants persisted in using the previous grasp type (overhand vs. underhand). All mentioned studies employed a binary measure of posture to demonstrate sequential effects. If, however, sequential effects result from the costs of replanning a movement, the forced choice (e. g. overhand vs. underhand) may have overstated their importance for motor planning. Therefore, Schütz and colleagues (2011) asked participants to open a column of drawers with cylindrical knobs, allowing for arbitrary pro/supination of the hand. Results showed that participants continuously modified their posture between drawers, but still exhibited a sequential effect for each drawer: In the descending sequences of trials, drawers were grasped with a more pronated posture than in the ascending sequences of trials. This suggests that the range of indifference is not a restricted range as may be deduced from the binary tasks, but instead the result of a trade-off between the costs of movement planning and the costs of movement execution, which precedes each movement.

We hypothesised that the executed movement is a weighted function of (1) the anticipated cognitive costs of creating a new movement plan and (2) the anticipated mechanical costs of executing a given motor task with the previous movement plan. In a sequential, binary task, within the range of indifference the mechanical costs are similar and weighted lower than the cognitive costs of creating a new movement plan. Once the mechanical costs of executing the given motor task with the previous movement plan exceed the cognitive costs, grasp type is switched and the range of indifference ends. In a sequential, continuous task, increasing the mechanical costs of the task should change the relative weight of the mechanical cost factor on movement execution and, thus, reduce the magnitude of the sequential effect.

To date, the question whether sequential effects are a cognitive property of the motor system (Rosenbaum et al., 2007) or simply a result of dynamical properties of the mechanical system (Kelso et al., 1994) is still unresolved. We asked whether the manipulation of the mechanical costs would establish a cognitive representation and, thus, influence the movement execution in an upcoming task. Retention of an attenuated sequential effect after removal of the additional mechanical costs would indicate the establishment of such a cognitive representation and, thus, provide support for the cognitive nature of sequential effects. To our knowledge, this is the first study which manipulates the mechanical costs of a given motor task to investigate the nature of sequential effects.

To approach these issues we created a sequential, continuous motor task, which offered means to increase the mechanical costs of the movements. Participants had to open a column of drawers with cylindrical knobs. The pro/supination angle of the hand at the moment of grasp was measured as the dependent variable. Drawers had to be opened in a randomised order in the warm-up, and in a sequential order in the pre-test, manipulation phase, and post-test. In the manipulation phase, the mechanical costs of opening and closing one of the drawers were increased by a mechanical brake. We hypothesised that a sequential effect would be present in the pre-test: Participants should use different postures for the ascending and descending sequences of trials. We further hypothesised that the magnitude of the sequential effect would be reduced in the post-test: Postures in the ascending and descending sequences of trials should differ less than in the pre-test. This attenuation of the sequential effect should be more pronounced for the weighted drawer. Posture in the randomised sequences of the warm-up should not be affected by sequential effects and, thus, differ from the postures in the ascending and descending sequences of the pre-test.

Methods

Participants

Twenty-three students (16 female, 7 male, mean age 23.9 years, age range 19–31 years) from Bielefeld University participated in the experiment. All participants were right handed (mean handedness score 0.95, all scores > 0.5) according to the revised Edinburgh inventory (Oldfield, 1971) and had normal mobility of the right hand, arm, and upper body. Participants characterised themselves as neurologically healthy and were naïve to the purpose of the study. Before the experiment, each participant provided his or her informed consent and read a detailed set of instructions concerning the required task. The participants did not receive financial compensation for their participation in the study. The study was in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki and approved by the local ethics committee.

Apparatus

The apparatus used was a tall metal frame (222 cm high, 40 cm wide, and 30 cm deep) with nine wooden shelves (see figure 3.1 a). A wooden drawer (8.5 cm high, 20 cm wide, and 30 cm deep) was placed on each shelf, with a number from 1 (lowest) to 9 (highest) inscribed on the left side. A stop mechanism allowed for a maximum pullout range of 21.5 cm. A plastic knob with a diameter of 7 cm and a depth of 4 cm was affixed to the centre of each drawer front.

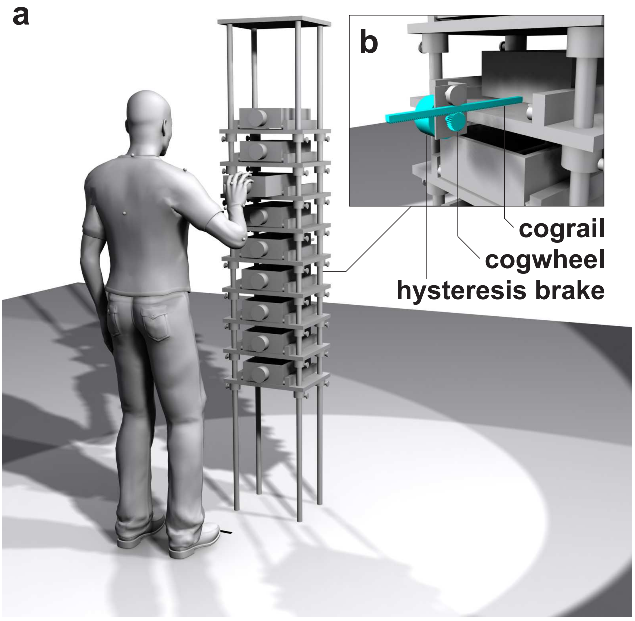

Figure 3.1: (a) Schematic of the experimental setup. The participant is positioned one arm length in front of the setup. Drawer #7 is set to shoulder height, drawer spacing is set to a quarter arm length. (b) Braking mechanism installed on the back of drawer #4. An opposing force of 25 N while opening and closing the drawer can be applied.

On the back of the fourth shelf a braking mechanism was installed. A cograil was affixed to the back of the drawer and actuated by a cogwheel attached to a current controlled hysteresis brake (see figure 3.1 b). A voltage of 14.9 V could be applied with a laboratory power supply. Application of current created an opposing force of 25 N (determined by previous calibration measurements with a load cell) while opening and closing the drawer. This was equivalent to lifting a weight of 2.5 kg.

Preparation

Each participant was tested individually. All reflective materials (e. g. watches, rings) had to be removed by the participant. Retro reflective markers (diameter 14 mm) were attached to ten bony landmarks of the thorax and right arm via palpation (see table 3.1).

The participant was positioned in front of the apparatus, arms stretched horizontally to the side and palms pointing towards the bookcase. The approximate height of the shoulder joint centre ($0.97 \times height\ of\ AC$, see table 3.1) and the arm length (distance between AC and RS, see table 3.1) of the participant were measured to normalise for the different body dimensions of the participants. The centre of drawer #7 was aligned to the height of the shoulder joint centre. The drawer spacing was set to $0.25 \times arm\ length$. The participant was positioned with his or her shoulder joint centre $1.00 \times arm\ length$ in front of the drawer face and $0.33 \times arm\ length$ to the left of the drawer centre. Two lines of tape were used to mark the normalised position of each participant in front of the apparatus: point of the toes and median plane of the body.

Procedure

The experiment consisted of four blocks, a warm-up, a pre-test, a manipulation phase, and a post-test. Before each block, the

Table 3.1: Anatomical landmarks, position and direction vectors used for the kinematic model.

Anatomical landmarks	
Code	Description
$C7$	*Processus spinosus* of the 7^{th} cervical vertebra
$T8$	*Processus spinosus* of the 8^{th} thoracic vertebra
IJ	*Incisuria jugularis* (deepest point)
PX	*Processus xiphoideus*
AC	*Articulatio acromioclaviculare* (most dorsal point)
EM	*Epicondylus medialis humeri*
EL	*Epicondylus lateralis humeri*
RS	*Processus styloideus radii*
US	*Processus styloideus ulnae*
MC	*Os metacarpale tertium* (dorsal of the *capitulum*)

Position and direction vectors		
Code	Description	Computation
WC	centre of the wrist joint	$(RS + US)/2$
$\mathbf{d_1}$	direction vector	$WC - MC$
$\mathbf{d_2}$	direction vector	$US - RS$
CC	centre of the *capitulum*	on a plane normal to $\mathbf{d_1} \times (\mathbf{d_2} \times \mathbf{d_1})$; 19.5 mm palmar from MC; $(MC - CC)$ and $(WC - CC)$ form right angle
$\mathbf{v}$	direction vector	$CC - WC$

correct positioning of the participant in front of the apparatus was controlled based on the floor marks.

In the warm-up, the participant had to open and close the drawers with the dominant right hand in five randomised sequences of trials, resulting in 45 trials (5 repetitions $\times$ 9 drawers). In the pre-test, manipulation phase, and post-test, the participant had to open and close the drawers with the dominant right hand in five ascending and five descending sequences of trials, resulting in 90 trials per block (2 sequences $\times$ 5 repetitions $\times$ 9 drawers). The sequences (ascending vs. descending) were alternated and the order of the sequences was counterbalanced across participants.

For the warm-up, a list of pseudo-random permutations of the drawer numbers was created before the experiment, based on the Mersenne twister algorithm (Matsumoto & Nishimura, 1998). Referring to this list, the experimenter announced each drawer to the participant. The participant started each trial from an initial position, with the arm hanging loosely on the side of the body, the palm of the hand touching the thigh. On the signal from the experimenter, the participant (1) raised the arm to the announced drawer, (2) closed the fingers around the knob, (3) opened the drawer to the full extent, (4) closed the drawer and (5) returned the arm to the initial position. Once the arm was back in the initial position, the experimenter announced the next drawer number. This sequence was repeated until all drawers had been attended to. After a short break of approximately 30 s, the participant started with the next sequence of trials and continued with this method until all five sequences of trials were completed.

In the pre-test, manipulation phase, and post-test, the experimenter only announced the order of the next sequence to the participant (‘from top to bottom’ vs. ‘from bottom to top’). The participant then executed all nine consecutive trials of the sequence on his or her own. Single trial execution was identical to the warm-up block. After a short break of 30 s, the experimenter announced the next sequence of trials until all ten sequences of the block had been attended to.

On completion of each block, an assistant asked the participant to step away from the apparatus to check the firm fit of the retro reflective markers. The experimenter meanwhile activated (after the pre-test) or deactivated (before the post-test) the hysteresis brake. Participants were not informed of the change. Experimental conditions were therefore identical in the pre- and post-test block, while participants had to surmount an opposing force of 25 N while opening and closing drawer #4 in the manipulation phase.
The entire experiment lasted approximately 50 min.

Motion Capture and Kinematic Analysis

Movement data were recorded using an optical motion capture system (Vicon Motion Systems, Oxford, UK) consisting of twelve MX-F20 CCD cameras with 200 Hz temporal and approximately 0.25 mm spatial resolution. The laboratory's coordinate system was defined with the $\mathbf{x}$-axis pointing to the right, the $\mathbf{y}$-axis pointing to the front, and the $\mathbf{z}$-axis pointing upwards while standing in front of the apparatus (see figure 3.2). Cartesian coordinates of the ten retro reflective markers were calculated from the camera data via triangulation. Marker trajectories were manually labelled and smoothed (Woltring filter, MSE 10 mm^2) in Vicon Nexus 1.4.116 and exported to MATLAB (2008b, The MathWorks, Natick, MA) for post processing.

For the calculation of the dependent variable, the pro/supination angle α of the hand at the moment of grasp, the projection of the hand onto the drawer face ($\mathbf{x}$-$\mathbf{z}$-plane) was used (see figure 3.2). The wrist joint centre (WC) was calculated halfway between RS and US (see table 3.1). Two direction vectors were defined, one pointing from the third metacarpal to the wrist joint centre ($\mathbf{d_1} = WC - MC$) and a second one passing through the wrist ($\mathbf{d_2} = US - RS$). The *capitulum* centre (CC) was then calculated on a plane normal to $\mathbf{d_1} \times (\mathbf{d_2} \times \mathbf{d_1})$. It was positioned palmar from MC at a distance of 19.5 mm (corresponding to

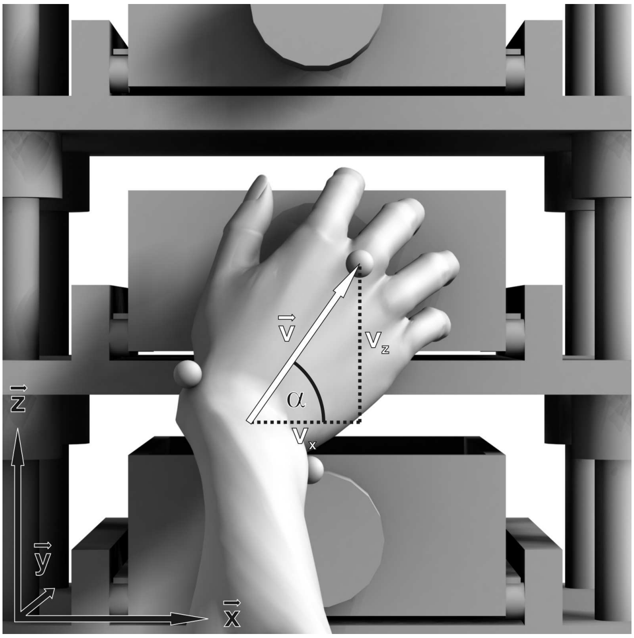

Figure 3.2: Measurement of the pro/supination angle α at the moment of initial grasp. For the calculation of α, the projection of the hand direction vector **v** onto the drawer face (**x**-**z**-plane) is used.

$0.5 \times \textit{average hand thickness} + \textit{marker radius}$) in a way that $(MC - CC)$ and $(WC - CC)$ formed a right angle.

A direction vector **v** was defined, pointing from the wrist joint centre to the *capitulum* centre ($\mathbf{v} = CC - WC$). The pro/supination angle α of the hand was calculated based on the vector components v_z and v_x, using the four-quadrant inverse tangent function integrated into MATLAB. The pro/supination angle was zero when **v** pointed directly to the right. Pronation of the hand caused an increase of the pro/supination angle, supination caused a decrease.

Data Analysis

To identify the moment of drawer grasp for each trial, the trajectory of the **y**-component (perpendicular to the drawer face, see figure 3.2) of the *capitulum* centre (CC) was analysed. Each trajectory started from a low initial value, corresponding to the initial posture of the participant, and exhibited two local maxima before returning to the initial value. The time of the first local maximum, corresponding to the moment of drawer grasp, was used to extract the associated pro/supination angle α of the hand.

For each of the 23 participants, 315 pro/supination angle values were measured, corresponding to 45 values (5 repetitions $\times$ 9 drawers) for the warm-up block and 90 values (2 sequences $\times$ 5 repetitions $\times$ 9 drawers) for each of the three remaining blocks, pre-test, manipulation phase, and post-test. The measurement values of all 23 participants were included in the analysis.

Results

Adequacy of the Selected Task

In order to provide evidence for an actual sequential effect in the selected task, we analysed the grasp postures of the ascending and descending sequences of trials in the pre-test, i. e. before the manipulation phase. To this end, we conducted a 2 (sequence: ascending vs. descending) $\times$ 5 (repetition) $\times$ 9 (drawer: lowest to highest) repeated measures ANOVA on the pro/supination angles. Where appropriate, the Greenhouse-Geisser correction was applied to the p-values; degrees of freedom, however, are reported uncorrected. The main effect of sequence was significant, $F(1, 22) = 24.901, p < .001$. Participants used a more supinated grasp in the ascending sequences and a more pronated grasp in the descending sequences (see figure 3.3). The main effect of drawer was also significant, $F(8, 176) = 1314.957, p < .001$. Participants used a more supinated grasp for the lower drawers and a more pronated grasp for the higher drawers. There was a significant interaction of sequence × drawer, $F(8, 176) = 15.368, p < .001$, such that pro/supination angle at each drawer was modulated differently by sequence. Post-hoc t-tests revealed significant differences in pro/supination angle as a function of sequence for the central seven drawers, $p_{2-8} < .05$. Participants used a more supinated grasp in the ascending sequences and a more pronated grasp in the descending sequences. The outermost two drawers, however, were not grasped differently depending on sequence, $p_{1,9} > .05$. Neither the main effect of repetition nor any remaining interaction was significant. Participants did not change their grasping behaviour over five repetitions.

Effect of the Manipulation

To examine the effect of the manipulation we conducted a 2 (condition: pre-test vs. post-test) × 2 (sequence: ascending vs. descending) × 5 (repetition) × 9 (drawer: lowest to highest) repeated measures ANOVA on the pro/supination angles. Where appropriate, the Greenhouse-Geisser correction was applied to the p-values; degrees of freedom, however, are reported uncorrected. The main effect of sequence, $F(1, 22) = 25.882, p < .001$, the main effect of drawer, $F(8, 176) = 1360.448, p < .001$, and the interaction of sequence × drawer, $F(8, 176) = 7.707, p < .001$, were significant, thus replicating the results of the pre-test. More importantly, there was a significant interaction of condition × sequence, $F(1, 22) = 11.320, p = .003$. Based on our hypothesis that the magnitude of the sequential effect would be reduced after the manipulation, we conducted a one-tailed t-test on the mean sequence-dependent difference in pro/supination angle. The sequence-dependent difference was significantly reduced from the pre- to the post-test, $t(22) = 3.365, p = .001$ (see figure 3.4). Pro/supination angles of the ascending and descending sequences of trials were more similar in the post-test. Participants showed less sensitivity to the sequential effect after the manipulation phase (see figure 3.5). Concerning the individual sequences, one-tailed t-tests neither showed a significant increase of the ascending values nor a significant decrease of the descending values from the pre- to the post-test, $p_{a,d} > .05$. We further found a significant interaction of condition $\times$ sequence $\times$ drawer, $F(8, 176), p = .002$. Post-hoc t-tests revealed that, in the post-test, an additional drawer (#3) was no longer grasped differently depending on sequence, $p_{1,3,9} > .05$. There was no main effect of repetition as well as no further interactions, indicating that participants did not change their grasping behaviour over five repetitions.

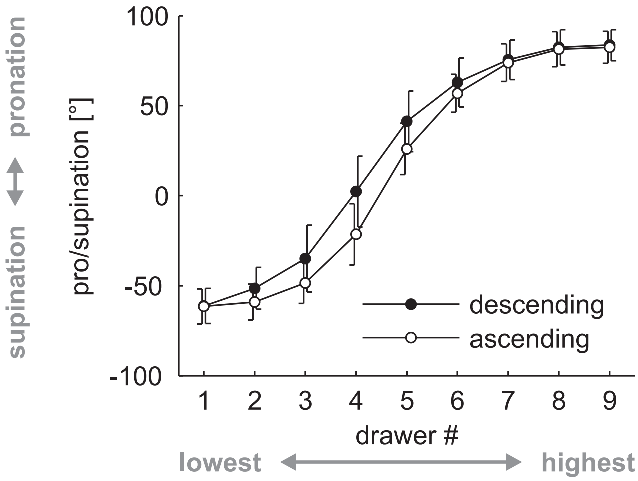

Figure 3.3: Pro/supination angle for the ascending and descending sequences of trials in the pre-test. Each data point represents the mean of all participants and repetitions for each drawer and movement direction, respectively. Error bars indicate standard deviation.

Effect of the Manipulation for the Weighted Drawer

To analyse the effect of the manipulation specifically for the weighted drawer we conducted a 2 (condition: pre-test vs. post-test) $\times$ 2 (sequence: ascending vs. descending) $\times$ 5 (repetition)

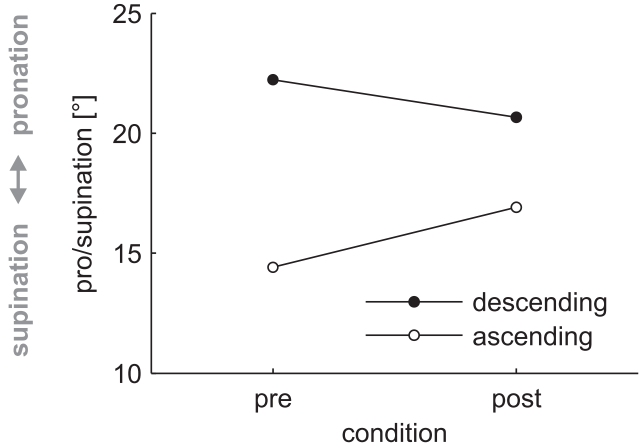

Figure 3.4: Comparison of the ascending and descending sequences of trials between pre- and post-test. Each data point represents the mean of all participants, repetitions, and drawers for each test condition.

repeated measures ANOVA on the pro/supination angles used at drawer #4. Where appropriate, the Greenhouse-Geisser correction was applied to the p-values; degrees of freedom, however, are reported uncorrected. The main effect of sequence was significant, $F(1, 22) = 26.764, p < .001$, replicating the results of the pre-test. We also found a significant interaction of condition $\times$ sequence for the weighted drawer, $F(1, 22) = 10.197, p = .004$. Based on our hypothesis that the magnitude of the sequential effect would be reduced after the manipulation, we conducted a one-tailed t-test on the sequence-dependent difference in pro/supination angle for the weighted drawer. The sequence-dependent difference was significantly reduced from the pre- to the post-test, $t(22) = 3.193, p = .004$ (see figure 3.6). Pro/supination angles of the ascending and descending sequences of trials were more similar in the post-test. Participants showed less sensitivity to the sequential effect after the manipulation phase. Concerning the individual sequences, one-tailed t-tests

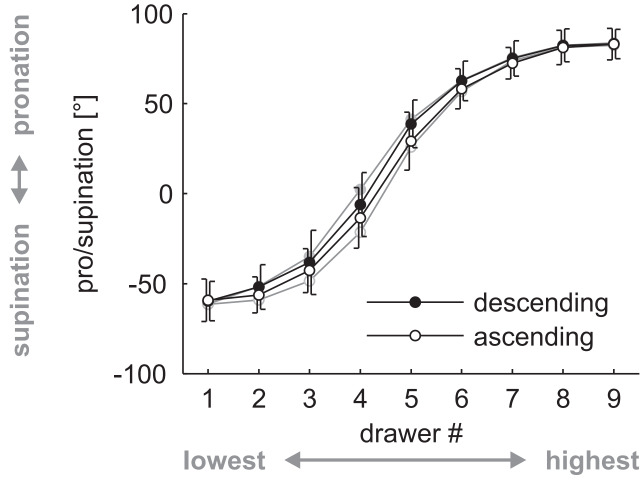

Figure 3.5: Black lines indicate pro/supination angle for the ascending and descending sequences of trials in the post-test. Each data point represents the mean of all participants and repetitions for each drawer and movement direction, respectively. Error bars indicate standard deviation. Grey lines indicate the results of the pre-test for comparison.

showed a significant increase of the ascending pro/supination angles, $t(22) = -1.983, p = .030$, as well as a significant decrease of the descending pro/supination angles, $t(22) = 2.960, p = .004$, from the pre- to the post-test. Hand pronation was reduced in the descending sequences and increased in the ascending sequences from the pre- to the post-test, bringing the sequence-dependent postures closer together.

Comparison of Sequential and Randomised Condition

To compare the pro/supination angles of the randomised and the sequential conditions we conducted unpaired t-tests between the randomised warm-up trials and the sequential trials from the pre-test. Results showed a significant difference between the randomised and the ascending sequences, $t(44) = 2.947, p = .005$,

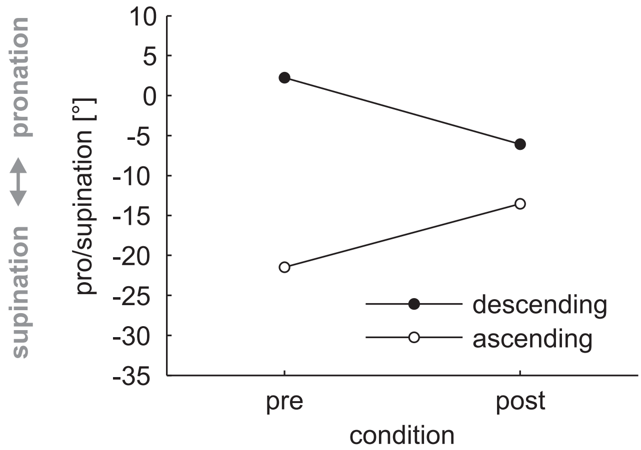

Figure 3.6: Comparison of the ascending and descending sequences of trials between pre- and post-test for the weighted drawer only. Each data point represents the mean of all participants and repetitions for each test condition.

indicating that participants used a more supinated grasp for the ascending trials than for the randomised trials (see figure 3.7). Results further revealed no significant difference between the randomised and the descending sequences, $t(44) = -0.293, p = .771$, indicating that grasp postures did not differ between these two conditions. Repeating the analysis for the randomised warm-up trials and the sequential trials from the post-test showed no significant differences, neither between the randomised and the ascending sequences, $t(44) = 1.873, p = .068$, nor between the randomised and the descending sequences, $t(44) = 0.304, p = .763$. Grasping behaviour under sequential conditions in the post-test did not differ significantly from the grasping behaviour under randomised conditions.

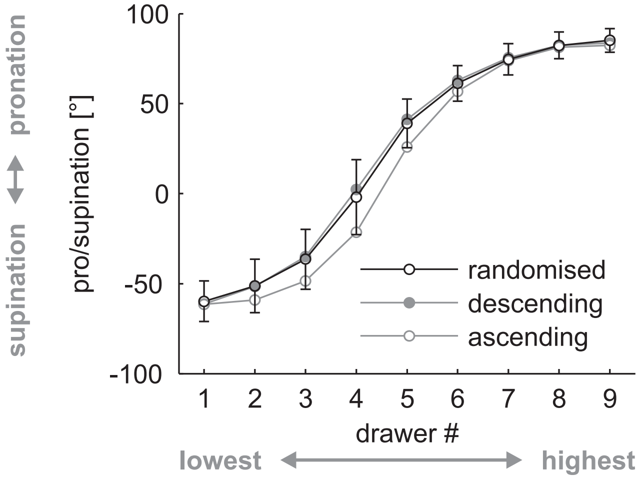

Figure 3.7: Pro/supination angle for the randomised sequences of trials compared to the ascending and descending sequences of trials in the pre-test. Each data point represents the mean of all participants and repetitions for each drawer and movement condition, respectively. Error bars indicate standard deviation.

Discussion

In the current study, we asked whether the anticipated mechanical costs of a movement would counteract the cognitive costs of movement planning and, thus, reduce the magnitude of the sequential effect. To this end, we created a sequential, continuous motor task (opening a column of drawers). A braking mechanism was installed to increase the mechanical costs of the task. We hypothesised that the sequential effect would be reduced after a manipulation phase with increased mechanical costs. Results showed that the magnitude of the sequential effect was significantly reduced after the manipulation phase.

The plan-modification-hypothesis (Rosenbaum et al., 2007) states that sequential effects result from the reuse of a former movement plan, thus reducing the planning cost of each movement in a sequential task. Sequential effects have been reproduced in a number of studies on hand trajectories (Diedrichsen et al., 2010; Jax & Rosenbaum, 2007; van der Wel et al., 2007) and binary changes of posture (Kelso et al., 1994; Rosenbaum & Jorgensen, 1992; Weigelt et al., 2009). Schütz and colleagues (2011) transferred these results to a continuous posture selection task, using a column of drawers with cylindrical knobs. The current study replicated and extended previous findings in an enhanced setup, where drawer heights and spacing were adjusted to the body dimensions of the participants. Participants exhibited a significant sequential effect in the pre-test, using a more pronated posture for the descending and a more supinated posture for the ascending sequences of trials.

The results of the pre-test also showed a significant interaction between sequence and drawer. Kelso and colleagues (1994) labelled the persistence effects found in their study *motor hysteresis*, a term originating from the field of physics. In physics, any system exhibiting hysteresis, i. e. path-dependence of its output signal, also shows a second property: A state of saturation reached for extreme input values, which causes convergence of the two path-dependent output signals (Mayergoyz, 1991). The pattern of results found in the current study demonstrates the same property for the motor system. The two path-dependent sequences of pro/supination angles converged for the two outermost drawers. Thus, persistence effects not only account for the main effect of sequence, but also for the significant interaction between sequence and drawer. A similar pattern of results was found in a previous study (Schütz et al., 2011), in which the path-dependent pro/supination angles converged for the lower, but not for the upper drawers. This difference may be due to the fact that the previous setup was not scaled to the body dimensions of the participants and, thus, the results were still influenced by biomechanical differences. Whereas the signal characteristics of the motor system support the use of the term motor hysteresis for these persistence effects, Kelso and colleagues (1994) specifically stated that motor hysteresis is an explicitly dynamical effect, that does not solely reflect features of the movement selection process as stated by Rosenbaum and Jorgensen (1992). Our results, however, proved that the reduced magnitude of the persistence effect was retained after the end of the manipulation phase, which indicates that a cognitive representation of the increased mechanical costs had been established. This finding demonstrates that the persistence effect found in the current study does not reflect dynamical but cognitive features of the motor system, thus supporting the use of the term *sequential effects* that was coined by Rosenbaum and Jorgensen (1992).

In their original study, Rosenbaum and Jorgensen (1992) suggested that sequential effects only occur within a range of indifference. Within this range, participants are equally content with either grasp type (overhand vs. underhand) and, thus, can reuse the previous motor plan to reduce planning costs. Several studies enforcing a binary change of posture (Kelso et al., 1994; Weigelt et al., 2009) support this notion. In a recent study (Schütz et al., 2011), participants were enabled to continuously modify their posture for each target. Results showed that sequential effects not only occurred within a limited range of indifference, but instead were present for the full sequence of trials. We hypothesised that sequential effects are a cognitive property of the motor system (Rosenbaum et al., 2007) and result from a trade-off between the cognitive costs of movement planning and the anticipated mechanical costs of the movement. To test this hypothesis, we increased the mechanical costs required to open a single drawer within the sequence, predicting a decrease in magnitude of the sequential effect and a retention of the decrease after removal of the mechanical cost manipulation. The result of the post-test showed that the magnitude of the sequential effect was significantly reduced compared to the pre-test. No significant effect of repetition was found in any of the task conditions. This indicates that the reduction of the sequential effect was caused by the manipulation of the mechanical costs and was not an effect of learning over time. The findings confirm our hypothesis that the anticipated mechanical costs of a movement counteract the cognitive costs of movement planning.

The initial experiment of Rosenbaum and Jorgensen (1992) demonstrated sequential effects for descending and ascending sequences of trials. Results of subsequent studies (Schütz et al., 2011; Short & Cauraugh, 1997) showed that sequential effects and, therefore, the reuse of motor plans, were absent in randomised sequences of trials. This finding suggests that differences in grasping behaviour should also be present between sequential orders of trials, which are influenced by sequential effects, and randomised orders of trials, which are not. This notion is supported by the study of Kelso and colleagues (1994), which qualitatively showed that the percentage of anti-phase grasps in a randomised task was between the percentages of anti-phase grasps in the sequential tasks. A study by Weigelt and colleagues (2009) showed that the point of change between overhand and underhand grasp in the randomised task was located between the points of change of the sequential tasks. However, two different participant groups were used for the randomised and the sequential experiments. None of the two studies mentioned above provided statistical evidence for these results. In the current study, we proved a significant difference between the randomised and the ascending sequences of trials in the pre-test, but no difference between the randomised and the descending sequences of trials. This pattern of results indicates that grasp selection in the descending sequences is similar to the randomised sequences and, therefore, not a result of sequential effects.

This finding may be an effect of the habitual system operating on the process of movement selection. Recent studies on the development of end-state comfort sensitivity over the lifespan demonstrated increased end-state comfort satisfaction with rising age (Stöckel et al., 2011; Thibaut & Toussaint, 2010; Weigelt & Schack, 2010). This result was present only if an underhand grasp was necessary for successful task performance, whereas task performance was equally high throughout all age groups for the overhand grasp condition. The authors (Stöckel et al., 2011; Weigelt & Schack, 2010) argued that the lower task performance in the underhand condition results from a competition between the goal oriented system (favouring the underhand grasp) and the habitual system (favouring the overhand grasp). In our experiment, partial control of grasp selection by the habitual system would favour a more pronated grasp in the randomised sequences and, thus, render them more similar to the descending sequences. At the same time, movements which are more strongly driven by the habitual system should have lower costs of movement planning. Therefore, the descending sequences should exhibit less sequential effect, which would render them more similar to the randomised sequences.

In conclusion, our findings demonstrate that sequential effects result from a trade-off between the costs of movement planning and the anticipated mechanical costs of the task. Increased mechanical costs change (1) the relative weight of the mechanical cost factor on movement execution and (2) the cognitive representation of upcoming mechanical costs. The increased weight of the mechanical cost factor in relation to the cognitive cost factor reduces the magnitude of the sequential effect in motor behaviour. Results further indicate that the magnitude of the sequential effect may be moderated not only by the goal oriented, but by the habitual system as well. Movements which are more strongly driven by the habitual system are less prone to exhibit sequential effects than others.

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Sequential Effects and Anticipation in a Virtual Pointing Task

CHAPTER 4

Abstract Over two decades ago the anticipation of subsequent postures and the persistence to previous postures in a sequential task were described for the first time. Since then, both effects have been reproduced in a large number of studies on reaching and grasping movements. We asked (1) whether sequential pointing movements would also be subject to these effects and (2) whether kinematic parameters of pointing in the physical environment could be reproduced in a virtual environment. To this end, we created a sequential, perceptual-motor task both in a physical and in a virtual environment. Participants were asked to point to a row of targets in the frontal plane in a sequential order. Results demonstrated that the kinematic parameters of the physical environment were faithfully reproduced in the virtual environment. Persistence effects were absent for posture and end-effector position in both environments. Anticipation, on the other hand, was demonstrated for posture both in the virtual and physical environment and for the end-effector position in the virtual task. To our knowledge, this anticipation of future positions in sequential tasks has not been demonstrated before.

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Introduction

A major step towards a better understanding of posture selection in reaching tasks was made by the comprehensive work of Rosenbaum and colleagues (Rosenbaum & Jorgensen, 1992; Rosenbaum et al., 1990). The authors described two common phenomena of reaching movements: the *end-state comfort effect* and the *sequential effect*. The original experiment on end-state comfort required participants to grasp a horizontal bar and to place one end on a target disk (Rosenbaum et al., 1990). Results showed that participants selected different initial postures depending on which end they intended to place on the target. By selecting awkward initial postures, participants ensured a comfortable posture at the end of the movement. End-state comfort has been reliably reproduced in a number of experiments on humans (Cohen & Rosenbaum, 2004; Hughes & Franz, 2008; Hughes, Reißig, & Seegelke, 2011; Seegelke, Hughes, & Schack, 2011; Short & Cauraugh, 1997, 1999; Weigelt, Cohen, & Rosenbaum, 2007; Weigelt, Kunde, & Prinz, 2006) and other primates (Chapman, Weiss, & Rosenbaum, 2010; Weiss, Wark, & Rosenbaum, 2007). Sensitivity to end-state comfort has been shown to develop over the lifespan (Stöckel, Hughes, & Schack, 2011; Weigelt & Schack, 2010). Different explanations have been postulated for the end-state comfort effect, such as the minimisation of time spent in awkward postures or the exploitation of potential energy (Rosenbaum & Jorgensen, 1992). Several studies support the *precision hypothesis* as a major factor behind the end-state comfort effect (Rosenbaum, Halloran, & Cohen, 2006; Rossetti, Meckler, & Prablanc, 1994; Short & Cauraugh, 1997, 1999). The precision hypothesis states that it is easier to make positioning movements well within the range of motion than near the extremes. In general, the end-state comfort effect demonstrates that subsequent postures are anticipated before movements are initiated. Anticipation is also found in prehension studies (Ansuini, Santello, Massaccesi, & Castiello, 2006; Armbrüster & Spijkers, 2006; Gentilucci, Negrotti, & Gangitano, 1997; Marteniuk, MacKenzie, Jeannerod, Athenes, & Dugas, 1987). The hand velocity profile of a prehension movement varies depending on whether the grasped object subsequently has to be thrown or placed (Armbrüster & Spijkers, 2006; Marteniuk et al., 1987). Both the shape and the orientation of the hand, as well as the finger positions on the object differ depending on subsequent task demands (Ansuini et al., 2006; Hesse & Deubel, 2010). All studies on end-state comfort and the anticipation of a subsequent movement state, however, were restricted to reaching tasks. To our best knowledge, no comparable results exist for pointing movements.

The second phenomenon of reaching movements described by Rosenbaum and Jorgensen (1992) was the sequential effect. Participants were asked to grasp a horizontal bar and to place its left or right end against one of 14 vertically aligned targets in a sequential order. Results showed that participants tend to stick to the previous grasp type (overhand vs. underhand). This sequential effect indicates that a movement plan is generated by modifications of a former plan (Rosenbaum, Cohen, Jax, Weiss, & van der Wel, 2007). Within a *range of indifference*, where participants are content with either grasp type, this modification causes less cognitive cost than the creation of a new movement plan. Sequential effects have been demonstrated in a number of studies on hand path (Diedrichsen, White, Newman, & Lally, 2010; Jax & Rosenbaum, 2007; van der Wel, Fleckenstein, Jax, & Rosenbaum, 2007). Diedrichsen and colleagues (2010), for example, showed that passive guidance of the hand along a task-redundant dimension induced a lasting modification of the hand path. Modifications of the posture are a prerequisite for such a modification of the hand path. Some studies therefore measured sequential effects of posture selection (Kelso, Buchanan, & Murata, 1994; Rosenbaum & Jorgensen, 1992; Weigelt, Rosenbaum, Hülshorst, & Schack, 2009). To simplify the description of the grasping behaviour, all of these studies were restricted to binary selection tasks (e. g. overhand vs. underhand grasp). In a complex environment, however, a grasp posture has to be selected from a continuous range of possible solutions. In a continuous task, the cognitive costs for both the creation of a new movement plan and the modification of a former movement plan might differ from those in a binary task. A recent study therefore extended research on sequential effects to continuous posture selection (Schütz, Weigelt, Odekerken, Klein-Soetebier, & Schack, 2011). Sequential effects were reproduced under continuous conditions, indicating that the results of binary tasks can be transferred to more complex environments. In a follow-up study, Schütz and Schack (2012) showed that increased mechanical costs in a continuous task reduce the magnitude of the sequential effect. The authors hypothesised that each executed movement is a weighted function of its cognitive and mechanical costs. Sequential effects result from the interplay of both cost factors. Posture selection rules like sequential effects and movement anticipation are required for all types of aimed limb movements. All mentioned studies, however, were restricted to reaching tasks. We therefore asked whether these posture selection rules would also apply to pointing movements.

Characteristics of pointing movements are well described in the literature. The target location of a pointing movement is encoded in local coordinates of the eye (Baud-Bovy & Viviani, 1998; Caminiti, Johnson, Galli, Ferraina, & Burnod, 1991; Kaminski & Gentile, 1989). Pointing precision is increased by online corrections (Crossman & Goodeve, 1983; MacKenzie, Marteniuk, Dugas, Liske, & Eickmeier, 1987; Prablanc, Echallier, Komilis, & Jeannerod, 1979; Schmidt, Zelaznik, Hawkins, Frank, & Quinn Jr, 1979), which are based on visual feedback (Adamovich, Berkinblit, Fookson, & Poizner, 1998, 1999; Adamovich, Berkinblit, Smetanin, Fookson, & Poizner, 1994; Soechting & Flanders, 1989). The hand path to the target location follows a roughly straight line in space and exhibits a smooth, bell-shaped velocity profile (Flash & Hogan, 1985; Morasso, 1981; Soechting & Lacquaniti, 1981). This hand path can be explained by the *equilibrium point hypothesis* (Bizzi, Accornero, Chapple, & Hogan, 1982; Flash, 1987; Hogan, 1984), which states that only the target posture of a movement has to be specified. The motor system sets the corresponding stiffness values for the antagonistic muscles of each joint. Spring-like properties of the muscles then drive the joints towards the point of force equilibrium. The equilibrium point hypothesis, however, does not address the problem of how the target posture is selected from a multitude of potential solutions. We therefore asked whether posture selection rules like movement anticipation and sequential effects would also apply to pointing tasks.

A number of pointing studies used visually and/or kinaesthetically memorised target locations (Adamovich et al., 1998, 1999, 1994; Soechting & Flanders, 1989). The use of virtual environments and visual online feedback of the target location, however, was so far limited to reaching movements. Several studies compared hand kinematics of reaching movements in virtual and physical environments (Bingham, Coats, & Mon-Williams, 2007; Cuijpers, Brenner, & Smeets, 2008; Hibbard & Bradshaw, 2003; Viau, Feldman, McFadyen, & Levin, 2004). Recent results showed that trajectories are similar in both environments, whereas speed and hand aperture differ (Magdalon, Michaelsen, Quevedo, & Levin, 2011). However, earlier findings indicated that speed and hand aperture in the virtual environment at least scale correctly with object size (Hibbard & Bradshaw, 2003). Bingham and colleagues (2007) demonstrated that accuracy and stereotypy of reaching movements can be reproduced in a virtual environment if a calibration with haptic feedback is allowed. These results indicate that virtual environments can be used for the study of reaching and grasping movements. To our knowledge, no comparable results exist for pointing movements. Thus, a second aim of our study was to compare kinematic parameters of pointing in the physical and virtual environment.

In the current study, we asked (1) whether sequential pointing movements would be affected by anticipation and/or sequential effects and (2) whether kinematic parameters of pointing movements would be faithfully reproduced in a virtual environment. To this end, we created a sequential, perceptual-motor task both in a virtual and in a physical environment. Participants were asked to point to a row of targets aligned in the frontal plane in a sequential order. We hypothesised that (1) sequential effects would be present in both the physical and virtual environment and that (2) hand orientation and position in the virtual environment would match those of the physical environment. Experiment 1 focused on anticipation and sequential effects in a virtual environment. In Experiment 2, the same phenomena were studied in the physical environment. Both experiments provide the basis to prove the occurrence of anticipation and sequential effects under varying reality conditions and to compare kinematic parameters of the virtual and physical environment.

Experiment 1

Participants

Eleven students (6 female and 5 male, mean age 23.1 years, age range 19–30 years) from Bielefeld University participated in the experiment in exchange for course credit. All participants were right handed (self-report) and had normal mobility of the right hand, arm, and upper body. Participants characterised themselves as neurologically healthy and were naïve to the purpose of the study. Before the experiment, each participant provided his or her informed consent and read a detailed set of instructions concerning the required task. The study was in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki and approved by the local ethics committee.

Setup

A height adjustable chair (34–47 cm high, seating area diameter 35 cm) was placed on a stack of four wooden plates (each 60 cm wide, 60 cm deep, and 4 cm high, see figure 4.1). Two to three additional wooden plates (60 cm wide, 30 cm deep, and 4 cm high) were placed in front of the chair to serve as a footrest for the participant. A projection screen (520 cm wide and 192 cm high) was installed in front of the participant at a height of 44 cm. The projection screen had a distance of 90 cm from the leading edge of the footrest. Virtual targets could be projected on the full surface area of the screen via two Canon XEED SX7 projectors (Canon Inc, Tokyo, Japan), creating a 118° field of view in the horizontal and a 63° field of view in the vertical direction. The targets were presented as complementary colour anaglyphs (red-cyan) and were computed online based on head tracking data. Each target consisted of a transparent cube with a crosshair in its centre.

Preparation

Each participant was tested individually. All reflective materials (e. g. watches, rings) had to be removed by the participant. Retro reflective markers (diameter 14 mm) were attached to eleven bony landmarks of the thorax and right arm via palpation (see table 4.1). The retro reflectively coated tip of a rubber glove was used as a marker for the index finger to permit natural pointing movements. The participant was equipped with a headband with four retro reflective markers for head tracking and a pair of anaglyph spectacles for the perception of the virtual targets. The participant was positioned on the chair, facing the projection screen. The height of the chair and the position of the participant on the chair were adjusted so that the shoulder marker (AC, see table 4.1) was at a predefined position in the lab coordinate system ($x = 0 \pm 20\,\text{mm}$, $y = 0 \pm 20\,\text{mm}$, $z = 1150 \pm 20\,\text{mm}$).

To ensure that the perceived positions of the virtual targets matched the predefined positions, two calibration steps were conducted: First, the participant was asked to stretch the right arm to the front, palm facing towards the screen, and spread the fin-

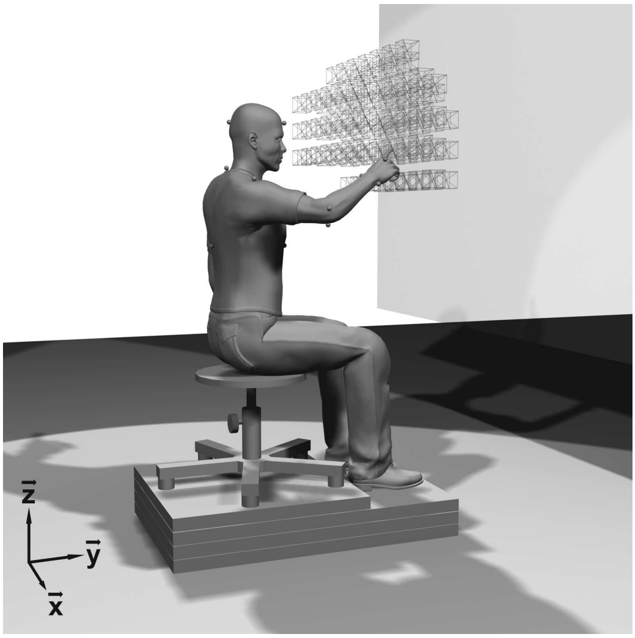

Figure 4.1: Schematic of Experiment 1, validation task. The participant faces the projection screen. The shoulder marker is located at a predefined position in the lab coordinate system. The 114 virtual target locations are depicted.

gers. Virtual targets were presented at the location of the index finger (TI) and thumb marker (TT). The participant had to indicate deviations in the **x**- and **z**-direction (see figure 4.1), which were corrected online by the experimenter. In the second step, the participant was asked to point to eight fixed targets and indicate when the finger was on the crosshair. Target locations formed a cube of side length 200 mm (centred at $x = -200$ mm, $y = 400$ mm, $z = 1350$ mm) in front of the participant. Based on the measured deviations in the **y**-direction, the eye-distance was calculated to match the depth perception of all participants.

Table 4.1: Anatomical landmarks used for marker placement.

Code	Description
C7	*Processus spinosus* of the 7^{th} cervical vertebra
T8	*Processus spinosus* of the 8^{th} thoracic vertebra
IJ	*Incisuria jugularis* (deepest point)
PX	*Processus xiphoideus*
AC	*Articulatio acromioclaviculare* (most dorsal point)
EM	*Epicondylus medialis humeri*
EL	*Epicondylus lateralis humeri*
RS	*Processus styloideus radii*
US	*Processus styloideus ulnae*
MC	*Os metacarpale tertium* (dorsal of the *capitulum*)
TI	Tip of the index finger
TT	Tip of the thumb

Validation Task

In the validation task, participants had to point to 114 target positions with their dominant right hand in four randomised sequences of targets, respectively. The order of targets was pseudo-randomised by the Mersenne twister algorithm (Matsumoto & Nishimura, 1998). The target volume was 720 mm wide, 360 mm high, and 270 mm deep and targets had a uniform spacing of 90 mm (see figure 4.1). The participant started each sequence from an initial position, with the right forearm resting on the right thigh and the palm facing downwards. On presentation of the first target, the participant (1) raised the arm to the target,

(2) placed the tip of the index finger in its centre and (3) remained in this position for 500 ms. After 500 ms, the target was switched off and the next target was presented. The participant was instructed to proceed directly to the next target. After twelve targets, the participant was asked to return to the initial position and pause until he or she was ready to continue. This procedure was repeated until all 114 targets of the sequence had been attended to. After a break of approximately 2 min, the participant started with the next sequence of targets.

Procedure

In the experimental task, participants had to point to twelve horizontally aligned target positions in the frontal plane with their dominant right hand. Participants executed four rightward and leftward sequences of trials, respectively (see figure 4.2). The sequences were alternated and the order of sequences was counterbalanced across participants. Targets had a uniform spacing of 90 mm and were presented at positions between $x = -540$ mm and $x = 450$ mm ($y = 440$ mm, $z = 1190$ mm, see figure 4.2).

The participant started each trial from the initial position, with the right forearm resting on the thigh and the palm facing downwards. On presentation of the first target, the participant (1) raised the arm to the target, (2) placed the tip of the index finger in its centre, (3) remained in this position for 500 ms until the target was switched off and (4) returned the arm to the initial position. This procedure was repeated until all targets had been attended to. After a short break of approximately 30 s, the participant started with the next sequence of trials.
The entire experiment lasted approximately 60 min.

Motion Capture

Movement data were recorded using an optical motion capture system (Vicon Motion Systems, Oxford, UK) consisting of twelve MX-F20 CCD cameras with 200 Hz temporal and approximately

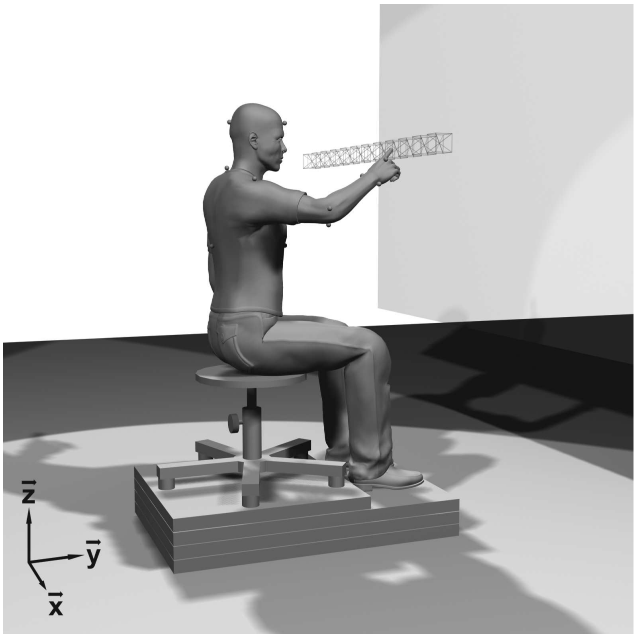

Figure 4.2: Schematic of Experiment 1, sequential task. The participant faces the projection screen. The shoulder marker is located at a predefined position in the lab coordinate system. The twelve virtual target locations in the frontal plane are depicted.

0.25 mm spatial resolution. The laboratory's coordinate system was defined with the **x**-axis pointing to the right, the **y**-axis pointing to the front, and the **z**-axis pointing upwards while facing the projection screen (see figure 4.2). Cartesian coordinates of the twelve retro reflective markers were calculated from the camera data via triangulation. Marker trajectories were manually labelled and smoothed (Woltring filter, MSE 10 mm^2) in Vicon Nexus 1.4.116 (Vicon Motion Systems, Oxford, UK) and exported to MATLAB (2008b, The MathWorks, Natick, MA) for post processing.

Kinematic Analysis

To derive a measure of posture which was comparable to previous studies on sequential effects, the projection of the hand onto the frontal plane ($\mathbf{x}$-$\mathbf{z}$-plane) was calculated (see figure 4.3 a). The wrist joint centre (WC) was calculated halfway between RS and US (see table 4.1). For the *capitulum* centre, two direction vectors were defined, one pointing from the third metacarpal to the wrist joint centre ($\mathbf{d_1} = WC - MC$) and a second one passing through the wrist ($\mathbf{d_2} = US - RS$). The *capitulum* centre (CC) was then calculated on a plane normal to $\mathbf{d_1} \times (\mathbf{d_2} \times \mathbf{d_1})$. It was positioned palmar from MC at a distance of 19.5 mm (corresponding to $0.5 \times \textit{average hand thickness} + \textit{marker radius}$) in a way that $(MC - CC)$ and $(WC - CC)$ formed a right angle. A direction vector $\mathbf{v}$ was defined, pointing from the wrist joint centre to the *capitulum* centre ($\mathbf{v} = CC - WC$). The pro/supination angle α of the hand was calculated based on the vector components v_z and v_x, using the four-quadrant inverse tangent function integrated into MATLAB. The pro/supination angle was zero when $\mathbf{v}$ pointed directly to the right. Pronation of the hand caused an increase of the pro/supination angle, supination caused a decrease.
As a measure for end-effector position, the $\mathbf{x}$-component of the index finger marker was used.

Data Analysis

To identify the moment of contact for each target, position and absolute velocity of the index finger marker (TI, see table 4.1) were calculated. For each sequence, the velocity profile exhibited twelve local minima within ±20 mm of target height. The frames of these minima were used to extract the pro/supination angle α of the hand and the position of the index finger marker. For each participant, 96 angles and positions were measured, corresponding to 2 (sequence) × 4 (repetition) × 12 (target) trials. All measurement values were included in the analysis.

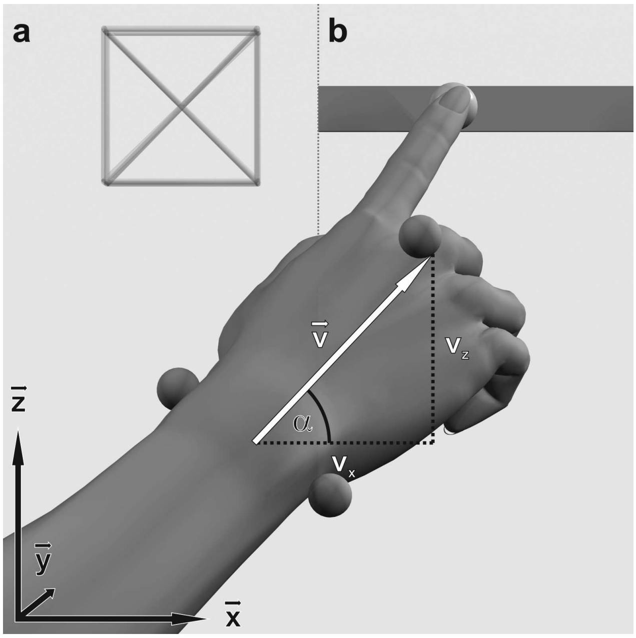

Figure 4.3: Measurement of hand orientation in the (a) virtual and (b) real condition. Direction vector **v** points from the wrist joint centre to the *capitulum* centre. Orientation α of the hand is calculated based on the vector components v_z and v_x (frontal plane).

Experiment 2

Participants

Fifteen students (7 female and 8 male, mean age 25.2 years, age range 23–30 years) from Bielefeld University participated in the experiment in exchange for course credit. All participants were right handed (mean handedness score 0.98, all scores > 0.5) according to the revised Edinburgh inventory (Oldfield, 1971) and had normal mobility of the right hand, arm, and upper body. Participants characterised themselves as neurologically healthy and were naïve to the purpose of the study. Before the experiment, each participant provided his or her informed consent and read a detailed set of instructions concerning the required task. The study was in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki and approved by the local ethics committee.

Setup and Preparation

The setup of the chair and wooden plates were identical to Experiment 1. Two metal stands with an aluminium bar (150 mm long, 15 mm square profile) on top were positioned in front of the chair (see figure 4.4). Twelve target balls (15 mm diameter) on steel pins (20 mm long) were attached to the front of the bar. The target balls had a uniform spacing of 90 mm. Two retro reflective markers on top of the bar were used to match the positions of the target balls to the positions of the virtual targets in Experiment 1. Positions were set between $x = -540$ mm and $x = 450$ mm ($y = 440$ mm, $z = 1190$ mm, see figure 4.4). The preparation was similar to Experiment 1. No headband or anaglyph spectacles were used and all steps concerning the calibration of the virtual environment were omitted.

Procedure

Procedure was similar to Experiment 1. Participants had to point to the twelve target positions with their dominant right hand in four rightward and leftward sequences of trials, respectively. The sequences were alternated and the order of sequences was counterbalanced across participants.

The participant started each trial from the initial position, with the right forearm resting on the thigh and the palm facing downwards. The order of the sequence was announced by the experimenter. The participant then (1) raised the arm to the first target, (2) placed the tip of the index finger on the target ball and (3) returned the arm to the initial position. This procedure was repeated until all targets had been attended to. After a

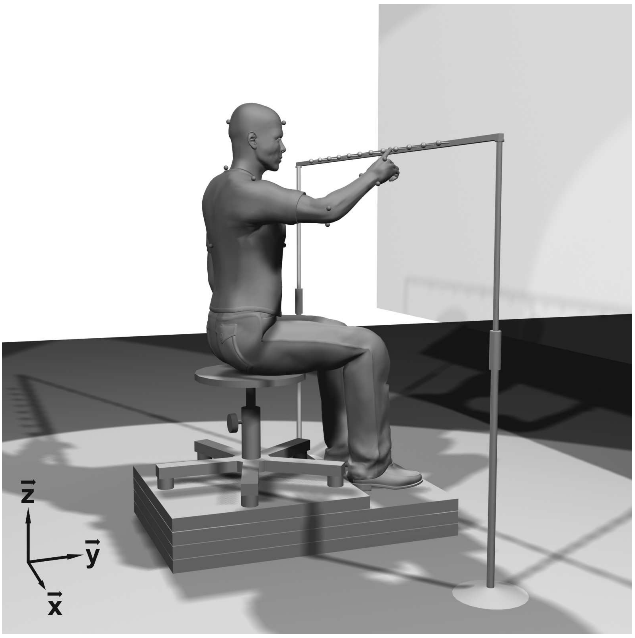

Figure 4.4: Schematic of Experiment 2. An aluminium bar with twelve target balls on steel pins is positioned in front of the participant. The shoulder marker is located at a predefined position in the lab coordinate system.

short break of approximately 30 s, the experimenter announced the order of the next sequence of trials.
The entire experiment lasted approximately 30 min.

Kinematic Analysis and Data Analysis

The same measure of posture as in Experiment 1 (projection onto the frontal plane) was used for the analysis (see figure 4.3 b). The pro/supination angle α was zero when $\mathbf{v}$ pointed directly to the right. Pronation of the hand caused an increase of the pro/supination angle, supination caused a decrease. As a measure for end-effector position, the $\mathbf{x}$-component of the index finger marker was used.

The same definition of contact was used as in Experiment 1. The according frames were used to extract the pro/supination angle α of the hand and the position of the index finger marker. For each participant, 96 angles and positions were measured, corresponding to 2 (sequence) $\times$ 4 (repetition) $\times$ 12 (target) trials. All measurement values were included in the analysis.

Results

Validation of the Visual Calibration

To render both experiments comparable, participants had to perceive the virtual targets at the predefined locations after the calibration procedure. The deviation between the predefined target position and the measured index finger position was calculated for each of the 114 virtual targets of the validation task in Experiment 1. The calculated deviations combined the perceptual errors of the targets and the positional errors of the motor system and the motion capture system. Figure 4.5 depicts the deviations in the **x**-, **y**-, and **z**-direction. The centre of the eight calibration targets was used as the zero position.

Linear regression analysis showed a highly significant correlation of deviation (d) and position (s) in all three dimensions:

$$
\begin{aligned}
d_x &= 0.018 s_x - 0.124\,\text{mm}, r_x^2 = 0.524, p_x < .001 \\
d_y &= 0.029 s_y + 0.098\,\text{mm}, r_y^2 = 0.447, p_y < .001 \\
d_z &= 0.021 s_z + 0.269\,\text{mm}, r_z^2 = 0.321, p_z < .001
\end{aligned}
$$

The regression equations indicate a deviation offset of less than a millimetre near the centre of the eight calibration targets and a linear deviation of less than 3 % in each dimension.

Anticipation and Sequential Effects

To analyse for anticipation and/or sequential effects we conducted a 2 (sequence) $\times$ 4 (repetition) $\times$ 12 (target) repeated

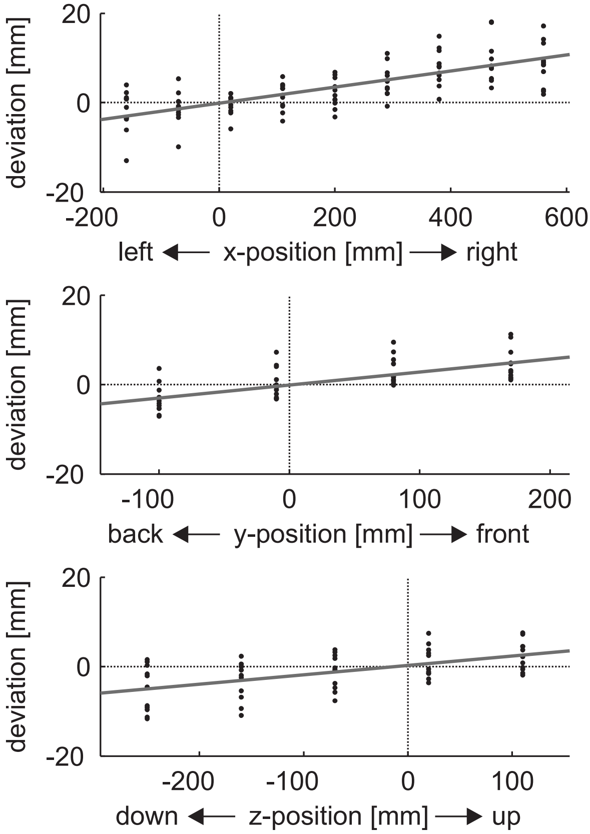

Figure 4.5: Deviation of predefined target position and measured end-effector position in **x**-, **y**-, and **z**-direction. The centre of the calibration targets was used as the zero position. Each data point represents one participant (mean of all targets in the specified plane).

measures ANOVA on (1) the pro/supination angles of the hand and (2) the end-effector positions, with experimental condition (virtual vs. real) as an inter subject factor. Where appropriate, the Greenhouse-Geisser correction was applied to the p-values; degrees of freedom, however, are reported uncorrected.

Both anticipation and sequential effects should result in a main effect of sequence, assuming that all targets were affected. If a limited number of targets were affected, an interaction of sequence $\times$ target should be present. If movements were subject to anticipation, they should tend towards the subsequent movement. For rightward sequences of trials, postures should be more supinated and end-effector positions should be shifted to the right. If movements were subject to sequential effects, they should tend towards the previous movement. For rightward sequences of trials, postures should be more pronated and end-effector positions should be shifted to the left.

Results for the pro/supination angle showed a significant main effect of target, $F(11, 264) = 978.266, p < .001$. Participants used a more pronated posture for the left targets and a more supinated posture for the right targets (see figure 4.6, black graphs). Pro/supination angle varied by $107.68 \pm 35.21°$ in the physical environment and by $115.95 \pm 38.82°$ in the virtual environment. There was a significant interaction of sequence $\times$ target, such that the posture at each target was modulated differently by sequence. Post-hoc t-tests demonstrated significant differences in pro/supination angles as a function of sequence for target #4, $t_4(25) = -2.294, p_4 < .05$, and target #5, $t_5(25) = -3.319, p_5 < .01$. Participants used a slightly more supinated posture in the rightward sequences and a slightly more pronated posture in the leftward sequences, indicating anticipation (see figure 4.6, grey graph). The posture for the remaining ten targets did not differ depending on sequence ($p_{1-3,6-12} > .05$). There was no significant effect of condition, $F(1, 24) = 0.127, p = .725$. Participants used the same postures for the virtual and the real targets.

Results for the end-effector position also showed no significant effect of experimental condition, $F(1, 24) = 0.071, p = .792$. Participants used the same positions for the virtual and the real targets. There was a significant main effect of sequence, $F(1, 24) = 33.771, p < .001$. The effect was modulated by

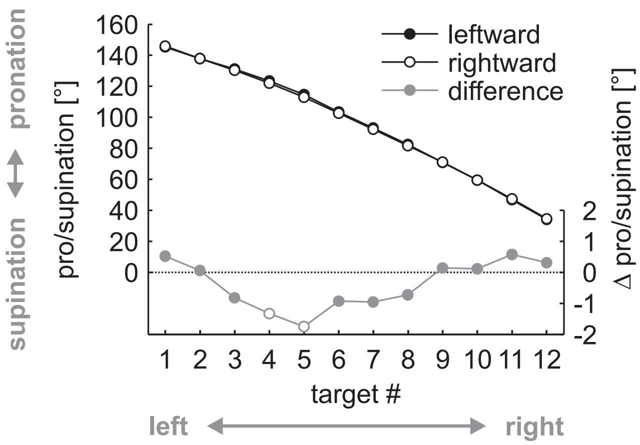

Figure 4.6: Pro/supination angle for the leftward and rightward sequences of trials (black graphs, left abscissa); rightward graph plotted on top, partially occluding leftward graph. Pro/supination angle difference (rightward − leftward) magnified by factor 20 (grey graph, right abscissa); white dots indicate significant differences from zero. Each data point represents the mean of 26 participants and four repetitions for each target.

a significant interaction of sequence × condition, $F(1, 24) = 31.559, p < .001$ (see figure 4.7). Post-hoc t-tests indicated that the position differed significantly depending on sequence for the virtual targets, $t(10) = 6.090, p < .001$, but not for the real targets, $t(14) = 0.188, p = 0.853$. Therefore, the virtual and the real target condition were analysed separately. For each condition, we conducted a 2 (sequence) × 4 (repetition) × 12 (target) repeated measures ANOVA on the end-effector position.

For the end-effector position in the virtual environment, results showed a significant main effect of target, $F(11, 110) = 47854.338, p < .001$, corresponding to the movement of the hand between the leftmost and rightmost target. More importantly, results showed a significant main effect of sequence, $F(1, 10) =$

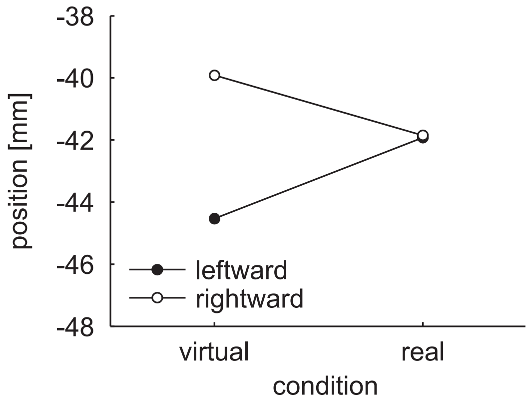

Figure 4.7: End-effector position for the leftward and rightward sequences of trials. Each data point represents the mean of twelve targets, four repetitions, and 11 (virtual condition) or 15 (real condition) participants.

$37.088, p < .001$. The position was shifted more to the right for rightward sequences and more to the left for leftward sequences of trials, indicating anticipation (see figure 4.8, grey graph). This effect was modulated by an interaction of sequence $\times$ target. Post-hoc t-test revealed that the end-effector position varied depending on sequence for all targets except target #7 ($p_7 > .05$).

For the end-effector position in the physical environment, results showed a significant main effect of target, $F(11, 154) = 130884.033, p < .001$, corresponding to the movement of the hand between the leftmost and rightmost target (see figure 4.9, black graphs). Neither the main effect of sequence, $F(1, 14) = 0.035, p = 0.853$, nor any interaction were significant, indicating that there was no shift of the position for the real targets.

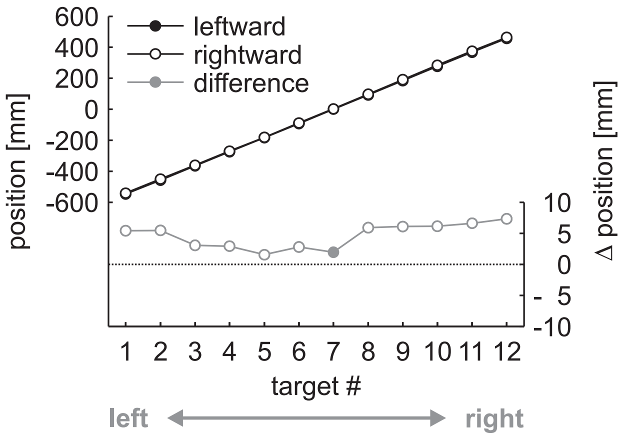

Figure 4.8: End-effector position for the leftward and rightward sequences of trials in the virtual condition (black graphs, left abscissa); rightward graph plotted on top, partially occluding leftward graph. Position difference (rightward − leftward) magnified by factor 20 (grey graph, right abscissa); white dots indicate significant differences from zero. Each data point represents the mean of eleven participants and four repetitions for each target.

Discussion

In the current study, we asked (1) whether sequential pointing movements were affected by anticipation or sequential effects and (2) whether kinematic parameters of pointing movements were faithfully reproduced in a virtual environment. To this end, we created a sequential, perceptual-motor task both in a virtual and in a physical environment. We hypothesised that sequential effects would be present in both environments and that hand orientation and position of the physical environment would be reproduced in the virtual environment. Results showed that the kinematic parameters of pointing movements did not differ in the virtual and physical environment. Findings further demonstrated that sequential effects were absent in both environments.

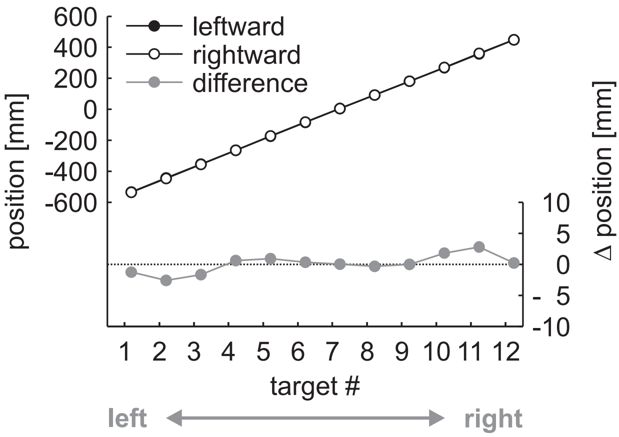

Figure 4.9: End-effector position for the leftward and rightward sequences of trials in the real condition (black graphs, left abscissa); rightward graph plotted on top, partially occluding leftward graph. Position difference (rightward − leftward) magnified by factor 20 (grey graph, right abscissa); white dots indicate significant differences from zero. Each data point represents the mean of 15 participants and four repetitions for each target.

On the other hand, anticipation effects were present for the hand orientation in both environments and for the hand position in the virtual environment.

To date, there are a number of studies which compared hand kinematics of reaching movements in virtual and physical environments (Bingham et al., 2007; Cuijpers et al., 2008; Hibbard & Bradshaw, 2003; Magdalon et al., 2011; Viau et al., 2004). Viau and colleagues (2004) found differences of arm postures between the virtual and the physical environment. The trajectories of reaching movements, on the other hand, were similar in both environments (Magdalon et al., 2011; Viau et al., 2004). All mentioned studies were restricted to reaching movements. In the present study, we asked whether virtual environments could also be used for the study of pointing movements. To this end, we analysed the orientation and position of the hand in a sequential pointing task. Results showed that, for pointing movements, neither orientation nor position of the hand differed significantly between environments. This finding supports the notion that virtual environments provide a valid tool for the investigation of pointing movements. Previous studies that investigated pointing movements towards virtual targets (Adamovich et al., 1998, 1999, 1994; Soechting & Flanders, 1989) found large deviations of the final hand position and the target location. The authors showed that no feedback-based corrections of the movement took place while pointing to virtual target locations. The mentioned studies, however, provided only kinaesthetic feedback of the target location. Results presented in the current study indicate that the large deviations previously found for virtual targets are absent if visual feedback of the virtual target location is available. This finding shows that visual feedback of the virtual targets is sufficient to evoke online corrections of the movement and, thus, contributes valuable information to the literature on aimed limb movements.

A second aim of the study was to verify whether pointing movements were subject to anticipation effects and/or sequential effects. We assumed that sequential effects would be present in the sequential pointing task. To date, sequential effects of posture have been reproduced in a number of studies on binary grasp selection (Kelso et al., 1994; Rosenbaum & Jorgensen, 1992; Weigelt et al., 2009). Schütz and colleagues (2011) further demonstrated sequential effects of posture selection in a continuous task space. All mentioned studies, however, were restricted to reaching movements. Results presented in the current study indicate that sequential effects are absent in a pointing task. This finding suggests that the same posture selection rules do not apply to all types of aimed limb movements. A possible explanation for the absence of sequential effects was provided in a recent study by Schütz and Schack (2012), which demonstrated that increased mechanical costs of a task reduced the magnitude of the sequential effect. The authors hypothesised that each executed movement is both a function of its anticipated cognitive and mechanical costs. Sequential effects result from the interplay of both factors. Based on this interpretation of sequential effects, decreased cognitive costs of a movement should also reduce the magnitude of the sequential effect. Whereas grasping necessitates the control of up to six degrees of freedom to translate and rotate the hand to match the position and orientation of the target object, in theory only three degrees of freedom are sufficient to translate the hand to a pointing target. Thus, pointing movements might indeed cause less cognitive planning costs, which in turn should improve the efficiency of motor planning and reduce the magnitude of the sequential effect. To corroborate this hypothesis, a systematic investigation of the number of independent degrees of freedom in reaching and pointing tasks should be the focus of further studies.

From an evolutionary point of view, one may speculate that reaching and grasping constitute phylogenetically older classes of movement, which are already observed in rodents (Whishaw, Pellis, & Gorny, 1992; Whishaw, Sarna, & Pellis, 1998). Pointing, on the other hand, might constitute one of the phylogenetically younger classes of movement. Pointing behaviour in the natural environment is observed only in the human species but not in other species of great apes (see Tomasello, 2006 for a review). Whereas some species of great apes with extensive human contact learn to point imperatively (i. e. to demand something), no declarative pointing (i. e. to direct attention) has ever been observed in great apes (Tomasello, 2006). On the other hand, both the end-state comfort effect (Chapman et al., 2010; Weiss et al., 2007) and sequential effects (Weiss & Wark, 2009) were demonstrated for non-human primates. This finding implies that these movement selection rules developed after the formation of grasping but before the formation of pointing movements. It is therefore possible that pointing movements are not affected by these rules of movement selection. One may speculate that pointing behaviour is either too young for some movement selection rules to be transferred from reaching to pointing or is not complex enough to require such rules.

Whereas no sequential effects (i. e. reuse of previous movement plans) were found in the current study, results still demonstrated a significant main effect of sequence on the hand position in the virtual task (see figure 4.8, grey graph). Effect direction did not support persistence to a previous, but anticipation of a subsequent hand position. Hand position was, on average, shifted to the right in rightward movement sequences, and to the left in leftward sequences. For hand orientation, a less pronounced anticipation effect was found, which was limited to two of the twelve target locations. The anticipation of a subsequent hand posture is well described in prehension studies. Shape and orientation of the hand, as well as the finger positions on a grasped object differ depending on the subsequent task demands (Ansuini et al., 2006; Hesse & Deubel, 2010). With regard to arm postures, the end-state comfort effect proves that participants accept awkward initial postures in order to avoid ending the movement sequence in an awkward posture (Cohen & Rosenbaum, 2004; Rosenbaum & Jorgensen, 1992; Rosenbaum et al., 1990; Short & Cauraugh, 1997, 1999). All previous studies on the anticipation of subsequent movement states, however, were restricted to reaching movements. The current study complements previous findings by demonstrating anticipation effects for the hand orientation in pointing movements. Furthermore, a significant anticipation effect was demonstrated for the position of the hand in the virtual target condition, which, to our knowledge, has not been described before.

In conclusion, our results demonstrate that virtual environments faithfully reproduce kinematic parameters of a sequential pointing task and, thus, provide a valid tool for the investigation of pointing movements. Results further show that sequential effects are absent in a sequential pointing task both for hand orientation and hand position. This finding indicates that the same set of posture selection rules does not apply to all types of aimed limb movements. On the other hand, anticipation effects are present for hand orientation in both the virtual and the physical environment, and for hand position in the virtual environment. To our best knowledge, anticipation effects for the hand position have not been demonstrated before.

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Motor Primitives of Pointing Movements in a Three-Dimensional Workspace

CHAPTER 5

Abstract A central question of motor control is how the motor system deals with redundant degrees of freedom. Redundancy can be reduced by coupling multiple degrees of freedom into a single motor primitive. Previous studies measuring motor primitives in aimed limb movements were restricted to two-dimensional target planes. We asked whether a limited number of motor primitives would also be sufficient to capture most of the data variance of aimed limb movements in a three-dimensional target volume. To this end, participants had to point towards virtual targets uniformly spaced in a three-dimensional workspace. Results showed that three motor primitives captured $87.4 \pm 3.1\,\%$ of the data variance of unrestrained pointing movements. Each motor primitive corresponded to a natural movement of the arm. The explained fraction of data variance did not differ from previous, two-dimensional studies. The findings imply that complex postures in a three-dimensional target volume can be reduced to three motor primitives. The reduction results in a unique mapping of target position and posture and, thus, solves the redundancy problem. The reduction further indicates that, in a pointing task, the motor system does not control hand rotation independent of hand translation.

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Introduction

Many of the seemingly simple tasks we conduct in our daily lives, such as reaching for and grasping an object, require a series of sensorimotor transformations which map the designated hand location to an appropriate muscle activation pattern. A number of these transformations have infinitely many valid solutions. The selection of a single solution thus results in an *ill-posed problem* for the motor system (Jordan & Wolpert, 1999). To generate the highly stereotypical behaviour found by experimental observation (Flash, 1987; Hogan, 1984), the motor system has to reduce the redundant degrees of freedom (Bernstein, 1967). Optimisation theory provides one computational approach for this reduction. The time-varying values that describe the movement are combined into a single optimality measure, such as minimum jerk (Hogan, 1984), minimum torque change (Uno, Kawato, & Suzuki, 1989), or minimum end-point variance (Harris & Wolpert, 1998).

An alternative way to reduce redundancy is to combine multiple degrees of freedom into a single *motor primitive* or *synergy* (Bernstein, 1967). The degrees of freedom in a motor primitive are no longer controlled individually but instead are coupled in their action. Muscle synergies have been reliably demonstrated in frog hind legs (d'Avella & Bizzi, 1998, 2005; d'Avella, Saltiel, & Bizzi, 2003), indicating a modular organisation of the frog's spinal cord circuitry. In human subjects, d'Avella and colleagues (2006) recorded electromyographic activity from 19 shoulder and arm muscles in a centre-out pointing task. Results showed that five muscle synergies were sufficient to explain 73–82 % of the data variance and that their amplitude coefficients were directionally tuned according to a cosine function. Such cosine tuning was also demonstrated for muscle synergies in the wrist joint (Haruno & Wolpert, 2005). Neurophysiological studies (Graziano, Aflalo, & Cooke, 2005; Graziano, Taylor, & Moore, 2002) revealed that electrical microstimulation of the motor cortex in monkeys evoked complex final postures, regardless of the required movement direction or muscle activation. This finding implied that postures are encoded directly in the motor cortex. Postural synergies were identified in several studies on human gait (Troje, 2002) and hand postures (Gentner & Classen, 2006; Grinyagin, Biryukova, & Maier, 2005; Santello, Flanders, & Soechting, 1998). Santello and colleagues (1998), for example, found that two motor primitives captured over 80 % of hand posture variance when grasping a large number of familiar objects. A number of studies investigated postural synergies of unrestrained arm movements. All of them, however, were either restricted to the sagittal (Berret, Bonnetblanc, Papaxanthis, & Pozzo, 2009; Latash, Aruin, & Shapiro, 1995; Thomas, Corcos, & Hasan, 2005) or horizontal plane (Debicki & Gribble, 2005; Sabatini, 2002). Bockemühl and colleagues (2010) sought to extend research on postural synergies of the arm to a three-dimensional workspace by using an unrestrained catching task. Results showed that three postural synergies captured 78–91 % of the data variance. Due to emergent properties of the catching task, though, target positions were again restricted to the frontal plane. We asked whether a similar fraction of the data variance would be captured by a limited number of motor primitives if targets were located in a three-dimensional workspace. To this end, participants had to point towards uniformly spaced targets in a virtual environment.

Pointing tasks are established means for the investigation of motor primitives (Berret et al., 2009; Latash et al., 1995). A reasonable number of characteristics of pointing movements have been described in the literature: The target location of a pointing movement is encoded in an external frame of reference (Baud-Bovy & Viviani, 1998; Caminiti, Johnson, Galli, Ferraina, & Burnod, 1991; Kaminski & Gentile, 1989). End-point precision at the target location is increased by online corrections (Crossman & Goodeve, 1983; MacKenzie, Marteniuk, Dugas, Liske, & Eickmeier, 1987; Prablanc, Echallier, Komilis, & Jeannerod, 1979; Schmidt, Zelaznik, Hawkins, Frank, & Quinn Jr, 1979), which are based on visual feedback (Adamovich, Berkinblit, Fookson, & Poizner, 1998, 1999; Adamovich, Berkinblit, Smetanin, Fookson, & Poizner, 1994; Soechting & Flanders, 1989). The hand path to the target location follows a roughly straight line in space and exhibits a smooth, bell-shaped velocity profile (Flash & Hogan, 1985; Morasso, 1981; Soechting & Lacquaniti, 1981). This hand path can be explained by the *equilibrium point hypothesis* (Bizzi, Accornero, Chapple, & Hogan, 1982; Flash, 1987; Hogan, 1984), which states that only the target posture of a pointing movement is specified through appropriate muscle stiffness values. Spring-like properties of the muscles then drive the joints towards the point of force equilibrium. A number of pointing studies used remembered target locations as virtual targets (Adamovich et al., 1998, 1999, 1994; Soechting & Flanders, 1989). The use of virtual environments and visual online feedback, however, was so far limited to reaching movements. Several reaching studies have compared hand kinematics in virtual and physical environments (Bingham, Coats, & Mon-Williams, 2007; Cuijpers, Brenner, & Smeets, 2008; Hibbard & Bradshaw, 2003; Magdalon, Michaelsen, Quevedo, & Levin, 2011; Viau, Feldman, McFadyen, & Levin, 2004). Hand trajectories, for example, are comparable in both environments, whereas movement speed and hand aperture differ (Magdalon et al., 2011). Earlier findings from Hibbard and Bradshaw (2003), however, imply that movement speed and hand aperture in the virtual environment at least scale correctly with object size. Bingham and colleagues (2007) demonstrated that accuracy and stereotypy of reaching movements can be reproduced in a virtual environment if a calibration with haptic feedback is allowed. These results indicate that virtual environments can be used for the study of reaching movements.

Schütz and Schack (2012b) extended this research to the study of pointing movements in virtual reality. Findings showed that both hand orientation and position of the physical environment were reproduced in the virtual environment. On the other hand, results demonstrated that *sequential effects* were absent in pointing tasks both in the physical and virtual environment. Sequential effects constitute a posture selection rule that has been reliably reproduced in reaching and grasping tasks using binary (Kelso, Buchanan, & Murata, 1994; Rosenbaum & Jorgensen, 1992; Weigelt, Rosenbaum, Hülshorst, & Schack, 2009) and continuous posture selection (Schütz & Schack, 2012a; Schütz, Weigelt, Odekerken, Klein-Soetebier, & Schack, 2011). According to the *plan-modification hypothesis* (Rosenbaum, Cohen, Jax, Weiss, & van der Wel, 2007), sequential effects result from the reuse of the previous movement plan and indicate that the motor system seeks to reduce the cognitive costs of movement planning. Recent findings (Schütz & Schack, 2012a), however, suggest that each executed movement is a weighted function of both its cognitive and mechanical costs. The motor system seeks to reduce not only the cognitive but the total movement costs. Sequential effects result from the interplay of both cost factors. Based on these findings, Schütz and Schack (2012b) hypothesised that the absence of sequential effects in pointing tasks results from lower cognitive costs in comparison to grasping. Whereas grasping necessitates the control of up to six degrees of freedom to translate and rotate the hand to match the available grip, in theory only three degrees of freedom are necessary to translate the hand to a pointing target. Up to now, no conclusive evidence for this reduction of the independently controlled degrees of freedom in a pointing task was provided. We therefore asked whether the number of motor primitives in a pointing task would match the number of independent degrees of freedom required for hand translation.

In the current study we address two issues that have been raised in previous studies on motor primitives and sequential effects: (1) whether a limited number of motor primitives is sufficient to capture most of the data variance of aimed limb movements in an actual three-dimensional workspace and (2) whether the number of motor primitives corresponds to the minimum number of independent degrees of freedom necessary for hand translation. To this end, we created a pointing task in a virtual environment. Participants were asked to execute pointing movements towards targets uniformly spaced in a three-dimensional workspace. We hypothesised that most of the data variance of unrestrained, three-dimensional pointing movements would be captured by only three motor primitives.

Methods

Participants

Eleven students (6 female and 5 male, mean age 23.1 years, age range 19–30 years) from Bielefeld University participated in the experiment in exchange for course credit. All participants were right handed (self-report) and had normal mobility of the right hand, arm, and upper body. Participants characterised themselves as neurologically healthy and were naïve to the purpose of the study. Before the experiment, each participant provided his or her informed consent and read a detailed set of instructions concerning the required task. The study was in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki and approved by the local ethics committee.

Setup

A height adjustable chair (34–47 cm high, seating area diameter 35 cm) was placed on a stack of four wooden plates (each 60 cm wide, 60 cm deep, and 4 cm high, see figure 5.1). Two to three additional wooden plates (60 cm wide, 30 cm deep, and 4 cm high) were placed in front of the chair to serve as a footrest for the participant. A projection screen (520 cm wide and 192 cm high) was installed in front of the participant at a height of 44 cm. The projection screen had a distance of 90 cm from the leading edge of the footrest. Virtual targets could be projected on the full surface area of the screen via two Canon XEED SX7 projectors (Canon Inc, Tokyo, Japan), creating a 118° field of view in the horizontal and a 63° field of view in the vertical direction. The targets were presented as complementary colour anaglyphs (red-cyan) and were computed online based on head tracking data. Each target consisted of a transparent cube with a crosshair in its centre.

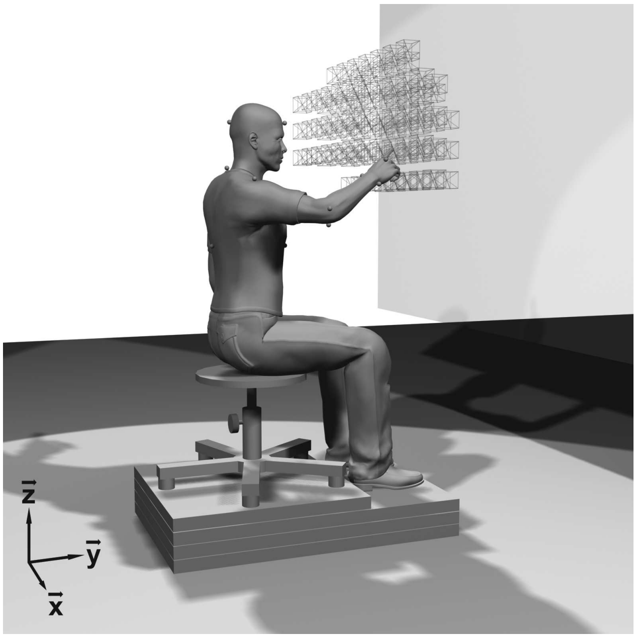

Figure 5.1: Schematic of the experimental setup. The participant faces the projection screen. The shoulder marker is located at a predefined position in the lab coordinate system. The 114 virtual target locations are depicted.

Preparation

Each participant was tested individually. All reflective materials (e. g. watches, rings) had to be removed by the participant. Retro reflective markers (diameter 14 mm) were attached to eleven bony landmarks of the thorax and right arm via palpation (see table 5.1). The retro reflectively coated tip of a rubber glove was used as a marker for the index finger to permit natural pointing movements. The participant was equipped with a headband with four retro reflective markers for head tracking and a pair of anaglyph spectacles for the perception of the virtual targets.

Table 5.1: Anatomical landmarks used for the kinematic model.

Code	Description
$C7$	*Processus spinosus* of the 7^{th} cervical vertebra
$T8$	*Processus spinosus* of the 8^{th} thoracic vertebra
IJ	*Incisuria jugularis* (deepest point)
PX	*Processus xiphoideus*
AC	*Articulatio acromioclaviculare* (most dorsal point)
EM	*Epicondylus medialis humeri*
EL	*Epicondylus lateralis humeri*
RS	*Processus styloideus radii*
US	*Processus styloideus ulnae*
MC	*Os metacarpale tertium* (dorsal of the *capitulum*)
TI	Tip of the index finger
TT	Tip of the thumb

The participant was positioned on the chair, facing the projection screen. The height of the chair and the position of the participant on the chair were adjusted so that the shoulder marker (AC, see table 5.1) was at a predefined position in

Table 5.2: Position and direction vectors.

Code	Description	Computation
WC	wrist joint centre	$(RS + US)/2$
EC	elbow joint centre	$(EM + EL)/2$
SC	shoulder joint centre	determined via sphere fitting in local coordinates of the clavicle
TU	top of the thorax	$(C7 + IJ)/2$
TL	bottom of the thorax	$(T8 + PX)/2$
TF	front of the thorax	$(IJ + PX)/2$
TB	back of the thorax	$(C7 + T8)/2$
$\mathbf{d_1}$	direction vector	$WC - MC$
$\mathbf{d_2}$	direction vector	$US - RS$
CC	centre of the *capitulum*	on a plane normal to $\mathbf{d_1} \times (\mathbf{d_2} \times \mathbf{d_1})$; 19.5 mm palmar from MC; $(MC - CC)$ and $(WC - CC)$ form right angle

the lab coordinate system ($x = 0 \pm 20\,\mathrm{mm}$, $y = 0 \pm 20\,\mathrm{mm}$, $z = 1150 \pm 20\,\mathrm{mm}$). The participant was asked to stretch the right arm to the side, palm facing towards the projection screen. Two movements of the shoulder (transverse adduction/abduction and extension/flexion) were recorded to calculate the shoulder joint centre (SC, see table 5.2).

To ensure that the perceived positions of the virtual targets matched the predefined positions, two calibration steps were conducted: First, the participant was asked to stretch the right arm to the front, palm facing towards the screen, and spread the fingers. Virtual targets were presented at the location of the index finger (TI) and thumb marker (TT). The participant had to indicate deviations in the **x**- and **z**-direction (see figure 5.1), which were corrected online by the experimenter. In the second step, the participant was asked to point to eight fixed targets and indicate when the finger was on the crosshair. Target locations formed a cube of side length 200 mm (centred at $x = -200$ mm, $y = 400$ mm, $z = 1350$ mm) in front of the participant. Based on the measured deviations in the **y**-direction, the eye-distance was calculated to match the depth perception of all participants.

The validity of this calibration procedure and the virtual environment was tested in Chapter 4. For each of the 114 virtual targets, the deviation of target position and index finger position was calculated. Regression analysis showed a deviation offset of less than one millimetre at the centre of the eight calibration targets and a linear deviation of less than 3 % in the **x**-, **y**-, and **z**-direction.

Procedure

Participants had to point to 114 target positions with their dominant right hand in four randomised sequences of targets, respectively. The target order was pseudo-randomised by the Mersenne twister algorithm (Matsumoto & Nishimura, 1998). The target volume was 720 mm wide, 360 mm high, and 270 mm deep and targets had a uniform spacing of 90 mm (see figure 5.1). The participant started each sequence from an initial position, with the right forearm resting on the right thigh and the palm facing downwards. On presentation of the first target, the participant (1) raised the arm to the target, (2) placed the tip of the index finger in its centre and (3) remained in this position for 500 ms. After 500 ms, the target was switched off and the next target was presented. The participant was instructed to proceed directly to the next target. After twelve targets, the participant was asked to return to the initial position and pause until he or she was ready to continue. This procedure was repeated until all 114 targets of the sequence had been attended to. After a break of approximately 2 min, the participant started with the next sequence of targets.
The entire experiment lasted approximately 45 min.

Motion Capture

Movement data were recorded using an optical motion capture system (Vicon Motion Systems, Oxford, UK) consisting of twelve MX-F20 CCD cameras with 200 Hz temporal and approximately 0.25 mm spatial resolution. The laboratory's coordinate system was defined with the $\mathbf{x}$-axis pointing to the right, the $\mathbf{y}$-axis pointing to the front, and the $\mathbf{z}$-axis pointing upwards while facing the projection screen (see figure 5.1). Cartesian coordinates of the twelve retro reflective markers were calculated from the camera data via triangulation. Marker trajectories were labelled and smoothed (Woltring filter, MSE 10 mm^2) in Vicon Nexus 1.4.116 (Vicon Motion Systems, Oxford, UK) and exported to MATLAB (2008b, The MathWorks, Natick, MA) for post processing.

Kinematic Analysis

Based on the anatomical landmarks (see table 5.1) the joint centres of the arm were calculated. Wrist and elbow joint centres were defined halfway between the associated marker positions (see table 5.2). For the hand centre, two direction vectors were defined, one pointing from the third metacarpal to the wrist joint centre ($\mathbf{d_1} = WC - MC$) and a second one passing through the wrist ($\mathbf{d_2} = US - RS$). The *capitulum* centre (CC) was then calculated on a plane normal to $\mathbf{d_1} \times (\mathbf{d_2} \times \mathbf{d_1})$. It was located palmar from MC at a distance of 19.5 mm (corresponding to $0.5 \times \textit{average hand thickness} + \textit{marker radius}$) so that $(MC-CC)$ and $(WC-CC)$ formed a right angle. The shoulder joint centre (SC) was defined based on the two calibration movements recorded for the shoulder joint in the preparation phase. Its position was calculated in local coordinates of the clavicle by a sphere fitting algorithm based on the elbow markers. Local segment coordinate systems were defined for the thorax, clavicle, humerus, forearm, and hand of the right arm (see table 5.3). Joint angles were calculated as Euler rotations between adjacent segments (see table 5.3), with the 2^{nd} and 3^{rd} rotation being defined in a moving frame of reference.

Data Analysis

Nine rotations, corresponding to anatomically valid degrees of freedom of the arm (see table 5.3), were used for the measurement of motor primitives. Each recorded frame was considered a single posture and, thus, corresponded to a point in nine-dimensional joint angle space. To restrict the analysis to postures within the target volume, movements executed towards or from the initial position were excluded from the data set. After data cleanup, on average $N = 75430(\pm 13970)$ postures remained for each participant, resulting in data sets of $N \times 9$ joint angles.

Motor primitives were calculated from the data sets by principal component analysis (PCA). PCA determines eigenvalues and eigenvectors of either the covariance or the correlation matrix of a data set. In the current study, a number of joints with little or no motion (e. g. the wrist) were present. To avoid the amplification of measurement noise in these joints by scaling, the covariance matrix was used for the PCA. The eigenvectors are aligned with the directions of largest variance and form the standard basis of a new orthonormal coordinate system. Each eigenvector is a principal component (PC) of the original data set. The coefficients of a PC represent the amount of coupling between the nine degrees of freedom. The associated eigenvalue of a PC equals its fraction of captured variance. If multiple degrees of freedom are combined in a motor primitive, their covariance is high. Thus, depending on the amount of coupling, a small number of PCs can be sufficient to capture most of the variance of the data set. According to the Kaiser-Guttman criterion (Jackson, 1993), PCs with an eigenvalue below 0.11 should be omitted from the analysis, as they would capture less variance than one variable of the original data set.

Table 5.3: Segment and joint angle definitions.

Local segment coordinate systems				
Description		**x**-axis	**y**-axis	**z**-axis
(a) thorax		$\mathbf{y} \times \mathbf{z}$	$(TB - TF) \times \mathbf{z}$	$TU - TL$
(b) clavicle		$(TL - TU) \times \mathbf{y}$	$IJ - SC$	$\mathbf{x} \times \mathbf{y}$
(c) humerus		$(EM - EL) \times \mathbf{y}$	$SC - EC$	$\mathbf{x} \times \mathbf{y}$
(d) forearm		$(US - RS) \times \mathbf{y}$	$EC - WC$	$\mathbf{x} \times \mathbf{y}$
(e) hand		$(US - RS) \times \mathbf{y}$	$WC - CC$	$\mathbf{x} \times \mathbf{y}$
Joint angle definitions				
Joint	Rotations	1^{st} rotation	2^{nd} rotation	3^{rd} rotation
$a \mapsto b$	z - y' - x''	clavicle pro/retraction	-	clavicle depression/elevation
$b \mapsto c$	z - x' - y''	shoulder transverse ad/abduction	shoulder extension/flexion	shoulder rotation medial/lateral
$c \mapsto d$	z - x' - y''	elbow flexion/extension	-	forearm pro/supination
$d \mapsto e$	z - y' - x''	wrist flexion/extension	-	wrist ad/abduction

Results

For the identification of motor primitives, PCA was applied to the data set of each participant. Each data set consisted of $N \times 9$ joint angles ($N = 75430 \pm 13970$ postures). Eigenvectors and eigenvalues of the covariance matrix were calculated. The first two PCs consistently satisfied the Kaiser-Guttman criterion; the third PC only satisfied the criterion in five participants (average eigenvalue 0.11 ± 0.02). This result indicates that the meaningful fraction of total variance is captured by two to three PCs. As a minimum of three PCs was required to represent the target volume, the third PC was included in the analysis for all participants.

Results showed that the first PC captured $50.6 \pm 5.5\,\%$ of the total variance, the second and third PC captured $25.5 \pm 4.7\,\%$ and $11.3 \pm 2.4\,\%$, respectively (see figure 5.2, grey graph). The first three PCs in combination captured $87.4 \pm 3.1\,\%$ of the data variance (see figure 5.2, black graph). This finding indicates that three PCs are sufficient to capture most of the data variance of pointing movements in a three-dimensional target volume. To evaluate this result, we calculated unpaired t-tests against comparable results of Bockemühl and colleagues (see Bockemühl et al., 2010, Fig. 6). No significant differences were found between the current results and the results of the previous study, $t_1(18) = 0.837, p_1 = .414$, $t_2(18) = 1.720, p_2 = .103$. Three PCs captured the same fraction of variance for a three-dimensional target volume as was previously demonstrated for targets restricted to the frontal plane.

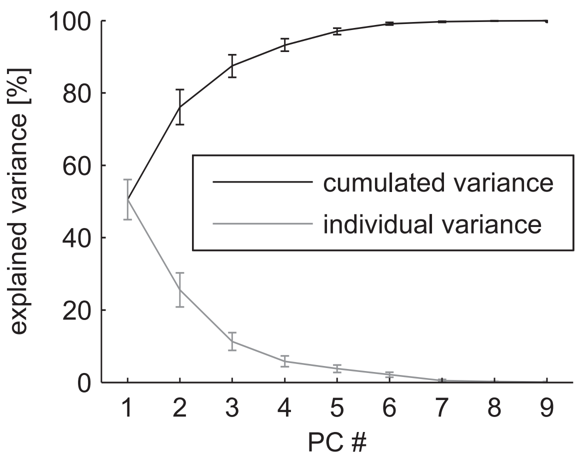

Figure 5.2: Individual (grey graph) and cumulated (black graph) fraction of total data variance captured by the nine PCs. Mean and standard deviation over eleven participants.

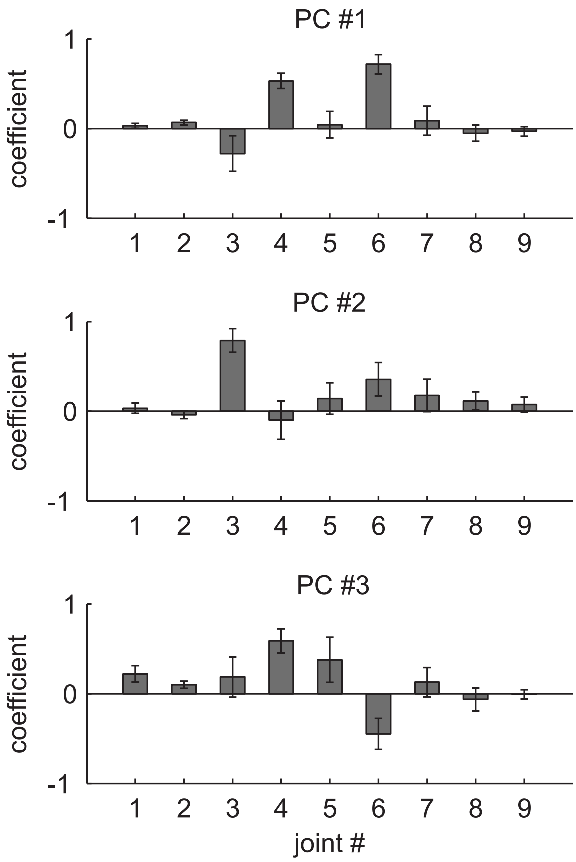

Figure 5.3: Coefficients of the first three PCs. Positive/negative sign corresponds to (1) clavicle pro/retraction (2) clavicle depression/elevation (3) shoulder transverse ad/abduction (4) shoulder extension/flexion (5) shoulder medial/lateral rotation (6) elbow flexion/extension (7) forearm pro/supination (8) wrist flexion/extension (9) wrist ad/abduction. Large absolute values of the coefficients indicate a high linear correlation.

The coefficients of each PC represent the amount of coupling between the nine joint angles. Large coefficients indicate a high linear correlation of joint angles. To simplify the description of the PCs, only coefficients with absolute values of over 0.25 and a significant difference from zero are reported. Coefficients of the first PC showed a strong coupling of shoulder transverse abduction, shoulder extension, and elbow flexion, coefficients of the second PC a coupling of shoulder transverse adduction and elbow flexion and coefficients of the third PC a coupling of shoulder extension, shoulder medial rotation, and elbow extension (see figure 5.3).

To visualise the effect of these couplings, three artificial movements were created. For each movement, the score of one of the first three PCs was modulated from +1.0 to −1.0 and the resulting postural change was superimposed on the average posture. For the first PC, modulation resulted in a movement from the back to the front, i. e. a bending and stretching of the arm (see figure 5.4). For the second and third PC, modulation resulted in a waving movement from left to right and from bottom to top, respectively. None of the movements resulted in unnatural postures of the arm. Each movement corresponds to one motor primitive.

Discussion

In the current study, we asked (1) whether a limited number of motor primitives would be sufficient to capture most of the data variance of aimed limb movements in a three-dimensional target volume and (2) whether the number of motor primitives would correspond to the minimum number of independently controlled degrees of freedom necessary for hand translation. To this end, participants executed a pointing task in a virtual environment. Virtual targets were spaced uniformly across a three-dimensional workspace. Results proved that three postural motor primitives captured most of the data variance of unrestrained pointing movements. Each motor primitive corresponded to a natural movement of the arm.

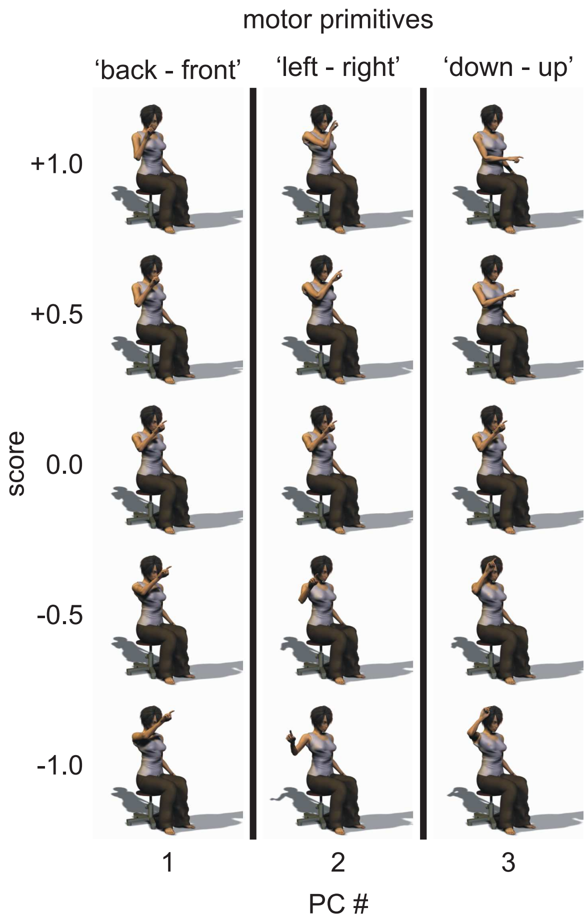

Figure 5.4: Artificial movements created by modulation of the score of each of the first three PCs from +1.0 to −1.0 and subsequent superposition of the postural change on the average posture. Each movement corresponds to one motor primitive.

Motor primitives of static postures have been identified in a number of studies on hand kinematics (Gentner & Classen, 2006; Grinyagin et al., 2005; Santello et al., 1998). Santello and colleagues (1998), for example, found that two motor primitives captured over 80 % of hand posture variance when grasping a large number of familiar objects. Their results proved that the control of hand postures involves only a few postural synergies. Many studies investigated motor primitives of unrestrained arm movements. All of them, however, were restricted to either the sagittal (Berret et al., 2009; Latash et al., 1995; Thomas et al., 2005) or horizontal plane (Debicki & Gribble, 2005; Sabatini, 2002). Bockemühl and colleagues (2010) sought to measure motor primitives of unrestrained catching movements in a three-dimensional target volume. Due to emergent properties of the selected task, however, target positions once again were restricted to the frontal plane. The current study extended these previous results by measuring motor primitives of pointing movements in a real three-dimensional workspace. Findings showed that three motor primitives captured most of the data variance of unrestrained pointing movements. Furthermore, a maximum of three motor primitives satisfied the Kaiser-Guttman criterion (Jackson, 1993) and, thus, explained a meaningful fraction of the data variance. The explained fraction of data variance did not differ significantly from that of a previous study (Bockemühl et al., 2010) restricted to a two-dimensional target plane. These findings imply that complex postures in a three-dimensional target volume can be reduced to a set of three motor primitives with limited loss of movement variance. This reduction results in a unique mapping of target positions and postures, which solves the ill-posed problem of selecting a single posture from multiple valid solutions (Bernstein, 1967). Motor primitives thus provide an efficient method to simplify movement control for the motor system.

Motor primitives of human arm movements have been demonstrated in several studies on muscle activation (d'Avella et al., 2006; Debicki & Gribble, 2005; Latash et al., 1995). D'Avella and colleagues (2006), for example, showed that a large fraction of the data variance of pointing movements in a centre-out task was captured by five muscle synergies. In this muscle-based approach, time-varying synergies had to be scaled in amplitude, shifted in time, and then combined linearly to reconstruct a muscle activation pattern. However, neurophysiological studies rather support a postural approach. Scott and colleagues (Scott, Gribble, Graham, & Cabel, 2001; Scott & Kalaska, 1997) demonstrated that activity in the primate motor cortex during reaching corresponded well to posture, but not to movement direction of the hand. In two subsequent studies, Graziano and colleagues (Graziano et al., 2005, 2002) were able to evoke complex postures by direct electrical microstimulation of the primate motor cortex. This implies that postures are directly encoded in the motor cortex. In the current study, we therefore measured joint angle synergies of static postures. Results indicate that, for unrestrained pointing in a three-dimensional workspace, three joint angle synergies capture most of the data variance. A single posture can be reconstructed as a simple linear combination of the scaled synergies. Movement reconstruction, on the other hand, still requires time-varying series of the scaling factors. Two different mathematical models might be used to address this issue. The *equilibrium point model* (Bizzi et al., 1982; Flash, 1987; Hogan, 1984) requires only the target posture to be specified through appropriate muscle stiffness values. Spring-like properties of the muscles then drive each joint to a corresponding point of force equilibrium. The *knowledge model* (Rosenbaum, Engelbrecht, Bushe, & Loukopoulos, 1993; Rosenbaum, Loukopoulos, Meulenbroek, Vaughan, & Engelbrecht, 1995), on the other hand, specifies the movement by interpolating between initial and target posture, using a bell-shaped velocity profile for each joint. The same interpolation method is applicable to the scaling factors of the motor primitives found in the current study. Our findings show that the scaling of each motor primitive results in a natural movement of the arm. Postural motor primitives might also resolve a remaining issue of the knowledge model: the large number of postures which have to be stored in memory (Rosenbaum et al., 1995). Results indicate that this large number of postures can be reduced to three motor primitives with limited loss of movement variance, thus offering a more efficient type of motor memorisation.

Schütz and Schack (2012b) demonstrated that sequential effects were absent in a sequential pointing task. This result was inconsistent with experiments on reaching and grasping, which reliably reproduced sequential effects in binary and continuous posture selection tasks (Kelso et al., 1994; Rosenbaum & Jorgensen, 1992; Schütz & Schack, 2012a; Schütz et al., 2011; Weigelt et al., 2009). Based on previous findings (Schütz & Schack, 2012a), the authors hypothesised that the absence of sequential effects in the pointing task results from the lower cognitive costs of pointing movements in comparison to grasping movements. Whereas grasping requires the control of up to six degrees of freedom to translate and rotate the hand to match the available grip, in theory only three degrees of freedom are needed to translate the hand to a pointing target. Up to now, no conclusive evidence for this hypothesis was provided. We asked whether the number of motor primitives in a pointing task would really be limited to the theoretical minimum of three independent degrees of freedom. Results showed that a major fraction of the data variance was captured by up to three motor primitives. This finding implies that the independent degrees of freedom in a pointing task are indeed limited to those required for hand translation. Consequently, hand rotation is not controlled independently but coupled directly to the hand translation. Our results thus support the hypothesis that the absence of sequential effects in pointing movements results from the lower cognitive costs (Schütz & Schack, 2012b). However, additional studies are required to prove that reaching and grasping involves a larger number of motor primitives than pointing.

In conclusion, our results demonstrate that three motor primitives capture a major fraction of the postural data variance of unrestrained, three-dimensional pointing movements. Thus, postures can be reduced to a set of three motor primitives with limited loss of movement variance. The reduction results in a unique mapping of target positions and postures and, therefore, provides a solution to the ill-posed problem of selecting a single posture from a multitude of valid solutions. The finding further proves that, in a pointing task, the motor system does not need to control hand rotation independent of hand translation.

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General Discussion

CHAPTER 6

The line of research described in the current thesis focuses on the investigation of rules for posture selection in reaching and pointing tasks. These rules include (1) the *end-state comfort effect*, which indicates the anticipation of a subsequent movement state, (2) *sequential effects*, which imply the reuse of a previous movement plan, and (3) *motor primitives*, which reduce the number of valid postures for a target location.

Both the end-state comfort effect and sequential effects have been reproduced in a number of studies restricted to binary posture selection (e. g. overhand vs. underhand grasp). The aim of Chapter 2 was to extend the research on these rules to posture selection in a continuous task space. To this end, a sequential, perceptual-motor task with a continuous range of posture solutions for each movement trial was created. Results showed that both the end-state comfort effect and sequential effects were present in the continuous task (see Chapter 2).

The *plan-modification hypothesis* states that sequential effects reduce the costs of movement planning within a *range of indifference*, where people are equally content with either grasp type. In a continuous task space, however, the concept of a restricted range of indifference is no longer viable. Hence, a revised interpretation of sequential effects was proposed. It was hypothesised that each executed movement is a weighted function of (1) the cognitive cost of movement planning and (2) the mechanical cost of movement execution. The motor system tries to optimise the total costs of each movement. Sequential effects result from the interplay of both factors. The aim of Chapter 3 was to corroborate this cost optimisation hypothesis. To this end, a sequential, continuous posture selection task was created. A braking mechanism was installed to increase the mechanical cost of movement execution. Findings showed that the magnitude of the sequential effects reduced as mechanical cost increased (see Chapter 3).

Sequential effects and the anticipation of a subsequent movement state have been demonstrated in multiple studies on reaching. Rules for selecting a single posture for a target location, however, are required for any type of aimed limb movement. The aim of Chapter 4 was to extend the research on both effects to pointing movements. For this purpose, a sequential pointing task was created in a virtual and in a physical environment. Results showed that sequential effects were absent in the pointing task. A significant anticipation effect was demonstrated for both hand orientation and hand position (see Chapter 4).

Motor primitives have been identified in numerous studies on muscle activation and posture, which were limited to two-dimensional target planes. The aim of Chapter 5 was to extend research on motor primitives to a three-dimensional target space. To this end, a three-dimensional pointing task was created in a virtual environment. Findings showed that three postural motor primitives explained most of the data variance of pointing movements. Thus, the number of motor primitives matched the dimensionality of the target space (see Chapter 5).

End-state Comfort

The end-state comfort effect indicates that the terminal posture of a movement is anticipated and incorporated into the motor plan. People select awkward initial postures in order to complete their movements in a more comfortable posture (Rosenbaum & Jorgensen, 1992; Rosenbaum et al., 1990). End-state comfort has been reliably reproduced in a number of experiments (Hughes & Franz, 2008; Hughes, Reißig, & Seegelke, 2011; Seegelke, Hughes, & Schack, 2011; Short & Cauraugh, 1997, 1999; Weigelt, Kunde, & Prinz, 2006). To simplify the description of the selected posture, all mentioned studies used a binary task (e. g. overhand vs. underhand grasp). In a complex environment, however, the motor system frequently has to select a single posture from a multitude of valid solutions. Only a small number of studies extended the research on end-state comfort to such non-binary posture selection. Haggard (1998) measured finger positions in an object rotation task to demonstrate that the initial wrist ad/abduction varies as a function of the object's target orientation. This finding was replicated in a continuous posture selection task by Zhang and Rosenbaum (2008). Both studies were focused on wrist ad/abduction. The binary posture selection used in a majority of previous end-state comfort studies, however, resulted from pro/supination movements of the wrist (cf. Rosenbaum, Cohen, Meulenbroek, & Vaughan, 2006). The experiment presented in Chapter 2 demonstrated the end-state comfort effect for continuous pro/supination movements of the wrist. This result supports the notion that previous findings obtained in binary tasks can be generalised to the continuous posture selection that is found in a complex environment. It is consistent with results published in parallel by Herbort and Butz (2010). The authors measured wrist pro/supination in a knob rotation task to confirm that the initial grasp posture varies as a function of the final knob orientation.

So far, studies investigating differences in end-state comfort preference between the dominant and non-dominant hand produced ambivalent results: In a bimanual end-state comfort task, Weigelt and colleagues (2006) found no hand specific differences of end-state comfort preference, whereas Janssen and colleagues (Janssen, Beuting, Meulenbroek, & Steenbergen, 2009; Janssen, Crajé, Weigelt, & Steenbergen, 2009) demonstrated such differences under more complex task conditions. Hughes and colleagues (2011) found no differences in end-state comfort preference between both hands, but a left-hand advantage for object transport times. In unimanual tasks, hand specific differences were demonstrated for the movement initiation time (Carson, Chua, Goodman, Byblow, & Elliott, 1995; Janssen, Crajé, et al., 2009). Hughes and Franz (2008), on the other hand, found neither differences in movement initiation time, nor differences in end-state comfort preference between both hands. The similarity in end-state comfort preference between hands was confirmed in a recent experiment (Seegelke et al., 2011). All mentioned results, however, were obtained in binary tasks. The restriction to binary grasp type selection may have concealed small postural differences. Therefore, in CHAPTER 2, the final postures of the dominant and non-dominant hand in a continuous posture selection task were compared. Results revealed no postural differences between both hands, implying that posture selection rules in a continuous task space operate equally on the dominant and non-dominant hand.

The end-state comfort effect describes a fundamental rule for posture selection in binary (Rosenbaum et al., 1990) and continuous tasks (Zhang & Rosenbaum, 2008). To achieve end-state comfort, the motor system has to anticipate the terminal posture of the movement even before the movement is initiated. Comparable effects have been described in studies on ideo-motor theory: The anticipated effect of a movement facilitates both its selection and initiation (Elsner & Hommel, 2001). Kunde (2001) further demonstrated that the representation of an anticipated effect is active before the movement is initiated. Anticipation of a subsequent movement state in a reaching movement was first described by Marteniuk and colleagues (1987). The authors showed that the velocity profile of a prehension movement varies depending on the precision demands of the subsequent movement. The peak velocity in the first segment of a two-stroke movement also differs depending on the precision demands of the second segment (Rand, Alberts, Stelmach, & Bloedel, 1997). With regard to posture, studies on object rotation suggest that the initial hand orientation varies as a function of the object's target orientation (Haggard, 1998; Zhang & Rosenbaum, 2008). Hesse and Deubel (2010) found a similar influence of the target orientation on the initial hand orientation, but also showed that the initial hand orientation is no longer affected by the target orientation if an intermediate task with high precision demands is introduced. All mentioned studies on end-state comfort and anticipation, however, were restricted to reaching tasks. The results presented in CHAPTER 4 demonstrate anticipation of a subsequent movement state in a sequential pointing task. Anticipation was found for hand orientation both in the virtual and physical environment. This finding is consistent with previous results on hand orientation (Hesse & Deubel, 2010) and indicates that movement anticipation applies to different types of aimed limb movements. An even more pronounced anticipation effect was found for the hand position in the virtual environment. To our best knowledge, this effect has not been described before.

Sequential Effects

Whereas the end-state comfort effect implies that subsequent movement states are incorporated into the movement planning process, sequential effects show that the previous movement state is incorporated as well. In a sequential, binary task, people stick to the previous posture (e. g. overhand vs. underhand grasp) for a range of targets (Rosenbaum & Jorgensen, 1992). This sequential effect has been reproduced in several binary studies (Kelso, Buchanan, & Murata, 1994; Weigelt, Rosenbaum, Hülshorst, & Schack, 2009). The plan-modification hypothesis states that the persistence to the previous posture reduces the cognitive costs of movement planning (Rosenbaum, Cohen, Jax, Weiss, & van der Wel, 2007). Within a range of indifference, where people are equally content with either posture, a new movement plan can be created by modification of the former plan. The modification causes lower cognitive costs than the creation of a new movement plan from scratch (Rosenbaum et al., 2007). To date, all experiments on sequential effects of posture selection were restricted to binary tasks. In a complex environment, however, the motor system has to select a single posture from a multitude of valid solutions. The cognitive costs for both the creation of a new movement plan and the modification of a former movement plan may therefore differ from those of a binary task. In Chapter 2, sequential effects were reproduced in a continuous task. Results showed that sequential effects in a continuous task are not limited to a range of indifference but operate on each executed movement to a different extent. These findings complement previous results on binary grasp type selection (Kelso et al., 1994; Rosenbaum & Jorgensen, 1992; Weigelt et al., 2009) and demonstrate that sequential effects constitute a fundamental rule for posture selection in binary and continuous tasks.

The plan-modification hypothesis interprets sequential effects as a rule to reduce the cognitive costs of movement planning within a limited range of indifference (Rosenbaum et al., 2007). The fact that sequential effects in the continuous task of Chapter 2 operated on each executed movement to a different extent, however, implied that this interpretation had to be revised. It was hypothesised that each executed movement is a weighted function of (1) the anticipated cognitive cost of creating a new movement plan from scratch and (2) the anticipated mechanical cost of executing the given motor task with the previous movement plan. The motor system seeks to optimise the total costs of the movement. Sequential effects result from the interplay of both cost factors. The aim of Chapter 3 was to corroborate this cost optimisation hypothesis. A sequential, continuous posture selection task (opening a column of drawers) was created. The mechanical cost of the task could be modified by a current controlled hysteresis brake attached to one of the drawers. If the hypothesis was correct, increased mechanical cost should change the relative weight of the mechanical cost factor on the executed movement and, thus, reduce the magnitude of the sequential effects. Results confirmed that the magnitude of the sequential effects was significantly reduced by increasing the mechanical cost. This outcome supports the hypothesis that each executed movement is a weighted function of both its cognitive and mechanical costs. This revised interpretation of sequential effects sheds new light on previous results obtained in binary tasks (Rosenbaum & Jorgensen, 1992; Short & Cauraugh, 1997). In a sequential, binary task, the grasp type should be switched once the anticipated mechanical cost of executing the task with the previous grasp type exceeds the anticipated cognitive cost of creating a new movement plan. This would lead to the range of indifference described by Rosenbaum and Jorgensen (1992). In a binary end-state comfort task, increased weight of the manipulated object should increase the relative weight of the mechanical cost factor on the executed movement. This would render the point of change between grasp types more pronounced, as was described by Short and Cauraugh (1997). The revised interpretation of sequential effects thus is in accordance with previous findings on posture selection in binary tasks.

The initial study by Rosenbaum and Jorgensen (1992) demonstrated sequential effects for ordered sequences of trials. Similar effects were shown for randomised sequences of trials in a study on hand path priming (Jax & Rosenbaum, 2007). Results by Short and Cauraugh (1997), on the other hand, indicate that sequential effects are absent in randomised sequences of trials. The authors, however, did not measure the effect of movement direction on posture selection but argued based on differences of grasp probability in comparison to Rosenbaum and Jorgensen (1992). In Chapter 2 the effect of movement direction on the selected posture was measured in randomised sequences of trials. The selected posture did not vary depending on movement direction. This result implies that sequential effects are discarded as a posture selection rule in randomised tasks and supports previous findings by Short and Cauraugh (1997). One may speculate that the absence of sequential effects is due to differences in cognitive costs between sequential and randomised tasks. Results of Chapter 3 indicate that each executed movement is a function of both its cognitive and mechanical cost and that the motor system seeks to minimise the total costs of the movement. The total costs of creating and executing a new movement plan should be constant. The cognitive cost of storing a previous movement plan should be constant as well, whereas the total costs of modifying and executing a previous movement plan should increase with the dissimilarity between the executed and the previous movement. Thus, the absence of sequential effects in the randomised task may indicate that (1) the high average dissimilarity of executed and previous movement causes the total modification costs to exceed those of creating a new movement plan or (2) the low probability that a previous movement plan can be reused does not compensate for the cognitive storage cost. Therefore, a systematic manipulation of either movement dissimilarity or reuse probability should be the focus of additional studies.

The results presented in Chapter 2 suggest that differences in posture selection should be present between sequential orders of trials, which are subject to sequential effects, and randomised orders of trials, which are not. This hypothesis is supported by previous results (Kelso et al., 1994), which indicated that the fraction of anti-phase grasps in a randomised task differs from the fraction of anti-phase grasps in a sequential task. A study by Weigelt and colleagues (2009) implied that the point of change of the grasp type in the randomised task is located between the points of change in the ascending and descending task. None of the mentioned studies, however, provided statistical evidence for these findings. In Chapter 3, a significant difference between randomised and ascending sequences of trials was demonstrated, complementing previous research on sequential effects. On the other hand, no difference between the randomised and the descending sequences of trials was found, indicating that posture selection in the descending sequences of trials is similar to that of the randomised sequences. Studies on the development of end-state comfort sensitivity over the lifespan (Stöckel, Hughes, & Schack, 2011; Weigelt & Schack, 2010) demonstrated that children exhibit less end-state comfort sensitivity if an underhand grasp is required for successful task performance. The authors argued that the lower performance results from a competition between the goal oriented (favouring the underhand grasp) and the habitual system (favouring the overhand grasp). The similarity between randomised and descending sequences of trials demonstrated in Chapter 3 supports the notion that posture selection is at least partially controlled by the habitual system.

The habitual system would (1) favour a more pronated posture in the randomised sequences of trials and (2) lower the cognitive costs of movement planning in the more pronated, descending sequences of trials. Lowered cognitive costs would reduce the magnitude of the sequential effects in the descending sequences and, thus, render them more similar to the randomised sequences.

For the sequential task in CHAPTER 3, setup dimensions and participant position were adjusted to the size and arm length of the participants. Thus, all influences of the body dimensions on posture selection were eliminated. Results revealed a sequential effect, but also demonstrated a significant interaction between sequence and drawer. Post-hoc t-tests revealed a sequential effect for the central drawers and convergence of the pro/supination angles for the outermost drawers. Kelso and colleagues (1994) labelled the persistence effects in their study *motor hysteresis*, a term originating from the field of physics. In physics, any system that exhibits hysteresis, i. e. path-dependence of its output signal, also reaches a state of saturation for extreme input values, which causes convergence of the path-dependent output signals (Mayergoyz, 1991). The pattern of results presented in CHAPTER 3 demonstrates the same property for the movement system, thus supporting Kelso's (1994) classification of these persistence effects as motor hysteresis. A similar pattern of results was already described in CHAPTER 2, where the path-dependent pro/supination angles converged for the lowermost, but not for the uppermost drawers. This difference may be due to the fact that the setup in CHAPTER 2 was not adjusted to the body dimensions of the participants and, thus, the measurements were still influenced by biomechanical differences.

The problem with the term motor hysteresis is that Kelso and colleagues (1994) specifically defined it as an explicitly dynamical effect, which does not solely reflect computational features of the movement selection process as proposed by Rosenbaum and Jorgensen (1992). The question whether the persistence effect of posture selection is a cognitive property of the motor system

(Rosenbaum & Jorgensen, 1992) or a dynamical property of the mechanical system (Kelso et al., 1994) is still unresolved. As a cognitive property, it should be labelled sequential effect; otherwise it should be labelled motor hysteresis. In a study on hand path priming (Jax & Rosenbaum, 2007), the authors proved that the persistence effect can be transferred to the contra lateral arm, supporting its cognitive nature. Results of Chapter 3 showed that a temporary increase of the mechanical costs induced lasting changes in movement execution: The magnitude of the persistence effect in the post-test (i. e. after the manipulation phase with increased mechanical costs) was significantly reduced relative to the pre-test. This retention of an attenuated persistence effect indicates that a cognitive representation of the increased mechanical costs was established and, thus, provides convincing support for the cognitive nature of the persistence effect proposed by Rosenbaum and Jorgensen (1992). Therefore, in the current thesis, the persistence effect of posture selection was labelled *sequential effect*, though the output characteristics of the motor system would support the term motor hysteresis as more fitting.

A potential shortcoming of all previous studies on sequential effects of posture selection (Kelso et al., 1994; Rosenbaum & Jorgensen, 1992; Weigelt et al., 2009) was their limitation to reaching tasks. Rules for selecting a posture from a multitude of valid solutions, however, are also a prerequisite for pointing movements. Characteristics of pointing movements have been described in numerous studies. For example, the target location of a pointing movement is encoded in an external frame of reference (Baud-Bovy & Viviani, 1998; Caminiti, Johnson, Galli, Ferraina, & Burnod, 1991; Kaminski & Gentile, 1989). Endpoint precision at the target is increased by online corrections based on visual feedback (Adamovich, Berkinblit, Fookson, & Poizner, 1998, 1999; Adamovich, Berkinblit, Smetanin, Fookson, & Poizner, 1994; Crossman & Goodeve, 1983; MacKenzie, Marteniuk, Dugas, Liske, & Eickmeier, 1987; Prablanc, Echallier, Komilis, & Jeannerod, 1979; Schmidt, Zelaznik, Hawkins, Frank, & Quinn Jr, 1979; Soechting & Flanders, 1989). The hand path to the target location follows a roughly straight line in space and exhibits a smooth, bell-shaped velocity profile (Flash & Hogan, 1985; Morasso, 1981; Soechting & Lacquaniti, 1981). This hand path can be explained by the *equilibrium point theory* (Bizzi, Accornero, Chapple, & Hogan, 1982; Feldman, 1966; Flash, 1987; Hogan, 1984), which requires only the target posture of a movement to be specified. The theory, however, does not address the problem of how this target posture is selected from a multitude of valid postures. The aim of Chapter 4 was to determine whether sequential effects, which constitute a fundamental rule for posture selection in reaching movements, would also apply to pointing movements. Results showed that no sequential effects were present for hand orientation and hand position in the pointing task.

One may speculate that reaching and grasping, which can already be observed in rodents (Whishaw, Pellis, & Gorny, 1992; Whishaw, Sarna, & Pellis, 1998), constitute phylogenetically older classes of movement. Pointing, on the other hand, might be one of the phylogenetically younger classes of movement: Pointing behaviour in the natural environment has only been observed in the human species but not in other species of great apes (cf. Tomasello, 2006). Whereas some species of great apes with extensive human contact can learn to point imperatively (i. e. to demand something), no declarative pointing (i. e. to direct attention) has ever been observed in great apes (Tomasello, 2006). On the other hand, both the end-state comfort effect (Chapman, Weiss, & Rosenbaum, 2010; Weiss, Wark, & Rosenbaum, 2007) and sequential effects (Weiss & Wark, 2009) were demonstrated for non-human primates. This implies that these movement selection rules developed after the formation of grasping but before the formation of pointing movements. It is therefore possible that pointing movements are subject to neither end-state comfort nor sequential effects. The absence of these rules, however, indicates that an alternative rule for posture selection has to be in effect for pointing movements.

Motor Primitives

Potentially, motor primitives can provide such an alternative rule to select a single posture for each target location. In a motor primitive, multiple degrees of freedom are coupled in their action. This coupling reduces the number of independent degrees of freedom (Bernstein, 1967). If the number of independent degrees of freedom is reduced to the dimensionality of the target space, motor primitives become a stand-alone rule for posture selection. A unique combination of the motor primitives then corresponds to each target location. In the human arm, motor primitives so far have mainly been demonstrated for muscle activation (d'Avella, Portone, Fernandez, & Lacquaniti, 2006; Debicki & Gribble, 2005; Latash, Aruin, & Shapiro, 1995). In a centre-out pointing task, for example, five motor primitives explained most of the data variance of the muscle activation patterns (d'Avella et al., 2006). To reconstruct the muscle activation patterns, these time-varying primitives were scaled in amplitude and shifted in time. Results of neurophysiological studies, though, rather support a postural approach of motor control (Scott, Gribble, Graham, & Cabel, 2001; Scott & Kalaska, 1997). Direct electrical microstimulation of the primate motor cortex evokes complex final postures, regardless of movement direction and joint torques (Graziano, Aflalo, & Cooke, 2005; Graziano, Taylor, & Moore, 2002). This finding indicates that postures are encoded directly in the motor cortex. In Chapter 5, motor primitives of pointing movements were identified on the level of static postures. Most of the data variance of unrestrained pointing movements is explained by three postural motor primitives. A single target posture can be reconstructed as a simple linear combination of the scaled motor primitives. Movement reconstruction, on the other hand, still requires time-varying series of the scaling factors. Two different mathematical models can be used to address this issue. The *equilibrium point model* (Bizzi et al., 1982; Feldman, 1966; Flash, 1987; Hogan, 1984) requires only a target posture to be specified. The movement itself is created by spring-like properties of the muscles. The *knowledge model* (Rosenbaum, Engelbrecht, Bushe, & Loukopoulos, 1993; Rosenbaum, Loukopoulos, Meulenbroek, Vaughan, & Engelbrecht, 1995) specifies the hand path by interpolating between initial posture and target posture, using a bell-shaped velocity profile for each joint. The same interpolation method is applicable to the scaling factors of motor primitives. Results presented in Chapter 5 show that the scaling of each motor primitive results in a natural movement of the arm. Postural motor primitives may also resolve a remaining issue of the knowledge model: the large number of postures which have to be stored in memory (Rosenbaum et al., 1995). Findings imply that this large number of postures can be reduced to three motor primitives with limited loss of movement variance, thus offering a more efficient type of motor memorisation.

To date, all studies investigating motor primitives of human arm movements used target locations in the sagittal (Berret, Bonnetblanc, Papaxanthis, & Pozzo, 2009; Latash et al., 1995; Thomas, Corcos, & Hasan, 2005), horizontal (Debicki & Gribble, 2005; Sabatini, 2002), or frontal plane (Bockemühl, Troje, & Dürr, 2010). Whereas target locations were restricted to two-dimensional planes, a minimum of three motor primitives was required to capture most of the variance of the posture data. Thus, the number of motor primitives exceeded the dimensionality of the target space. For motor primitives to become a standalone rule to select a single posture for each target position, the number of motor primitives has to match the dimensionality of the target space. Results of Chapter 5 demonstrated that three motor primitives capture most of the data variance of unrestrained pointing movements in a three-dimensional target space. Furthermore, a maximum of three motor primitives satisfy the Kaiser-Guttman criterion (Jackson, 1993) and, thus, explain a meaningful fraction of the total data variance. These results confirm that, for pointing movements, the number of motor primitives matches the dimensionality of the target space. This direct matching results in a unique solution to the transformation of target position and posture. Motor primitives thus provide a stand-alone rule for posture selection, which can replace other posture selection rules such as end-state comfort and sequential effects. The results presented in Chapter 5 therefore explain the absence of sequential effects in pointing movements, which was demonstrated in Chapter 4.

One may speculate that the number of independent degrees of freedom constitutes the main difference between reaching and pointing movements. For a reaching movement, the motor system requires up to six independent degrees of freedom: Both the hand rotation and the hand position have to match the orientation and position of the manipulated object. For a pointing movement, on the other hand, only three independent degrees of freedom are required to translate the hand to the target location. In Chapter 5, motor primitives of unrestrained pointing movements were identified in a three-dimensional target space. Each motor primitive can be considered an independent degree of freedom of the arm. Results showed that only three motor primitives captured a meaningful fraction of the data variance (Jackson, 1993). These three motor primitives correspond to the theoretical minimum of independent components required for the translation of the hand in the three-dimensional target space. Thus, hand rotation is not controlled independently but coupled to hand translation. This result supports the hypothesis that pointing movements involve fewer independent degrees of freedom than reaching movements. One can assume that motor primitives constitute a basic mechanism to reduce the number of independent degrees of freedom in all types of aimed limb movements. For pointing movements, this reduction can result in a unique solution to the transformation between target position and posture, which renders additional posture selection rules unnecessary. For reaching movements, however, up to six independent degrees of freedom are required to satisfy task demands, which exceeds the dimensionality of the target space. Therefore, additional posture selection rules such as the end-state comfort effect and sequential effects are required to control the redundant degrees of freedom.

To conclude, the findings of Chapter 2 demonstrate that the end-state comfort effect and sequential effects constitute fundamental rules for posture selection in binary and continuous tasks. In a continuous task, sequential effects are not limited to a range of indifference but operate on each executed movement to a different extent. Based on this outcome, the cost optimisation hypothesis was proposed as a revised interpretation of sequential effects. The hypothesis states that each executed movement is a weighted function of its anticipated cognitive and mechanical costs. The motor system seeks to optimise the total costs of each movement. Sequential effects result from the interplay of both cost factors. The results shown in Chapter 3 corroborate this hypothesis. Findings further imply that partial involvement of the habitual system in movement planning reduces the cognitive costs and, thus, the magnitude of sequential effects. The findings of Chapter 4 demonstrate that sequential effects are absent in pointing movements. This result proves that not all posture selection rules apply to every type of aimed limb movement. An alternative rule for posture selection has to be in effect for pointing movements. The results discussed in Chapter 5 imply that postures in a three-dimensional pointing task can be reduced to three motor primitives. Thus, motor primitives serve as a standalone rule for posture selection in pointing tasks, which renders additional selection rules such as sequential effects unnecessary. The work presented in this thesis reviewed different rules for the selection of postures. The transfer of these rules to a continuous task space provided new insights into the posture selection process and deepened our understanding of the underlying cognitive principles of human motor control.

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Summary

CHAPTER 7

For even the simplest movements, our sensory input and motor output are closely linked. Early work in psychology suggests that this link results in a bidirectional association between the movement and its sensory effect, which can be used for movement selection and initiation. A number of the motor transformations that are required for movement selection, however, have multiple solutions. This redundancy would prevent the formation of bidirectional associations. Thus, additional rules are required to select a single solution for each motor transformation. In the current thesis, three rules that contribute to posture selection were addressed: (1) the *end-state comfort effect*, which indicates the selection of a comfortable terminal posture, (2) *sequential effects*, which imply the reuse of a previous posture, and (3) *motor primitives*, which reduce the number of available postures.

The aim of Chapter 2 was to determine whether the end-state comfort effect and sequential effects would be reproduced in a continuous posture selection task. To this end, a sequential, perceptual-motor task was designed, which offered a range of valid postures for each movement trial. Participants had to open a column of drawers with cylindrical knobs in a sequential order. Results showed that the end-state comfort effect and sequential effects were reproduced in a continuous task space, thus supporting their generality as posture selection rules. Findings further demonstrated that sequential effects are not limited to a *range of indifference* but operate on each executed movement to a different extent. This result implied that the interpretation of sequential effects had to be revised.

In Chapter 3, a revised interpretation of sequential effects was proposed. It was hypothesised that each executed movement in a sequential task is a weighted function of (1) the anticipated cognitive cost of movement planning and (2) the anticipated mechanical cost of movement execution. The motor system seeks to optimise the total movement costs. Sequential effects result from the interplay of both cost factors. To corroborate this cost optimisation hypothesis, the sequential, perceptual-motor task of

Chapter 2 was modified. A braking mechanism was installed on one of the drawers to increase the mechanical cost of the task. According to the hypothesis, increased mechanical cost should reduce the magnitude of the sequential effects. Results showed that the magnitude of the sequential effects was significantly reduced after a manipulation phase with increased mechanical cost. This finding confirmed that sequential effects are a cognitive feature of the movement selection process and result from the interplay of two cost factors. Results further indicated that partial involvement of the habitual system in movement planning can reduce the cognitive cost and, thus, the magnitude of the sequential effects.

The aim of Chapter 4 was to verify whether sequential effects would apply to all types of aimed limb movements. To this end, a sequential pointing task was created in a virtual and in a physical environment. Participants had to point to a row of targets in the frontal plane in a sequential order. Results showed that no sequential effects were present in this task. This finding suggested that the same posture selection rules do not apply to every type of aimed limb movement. Therefore, an alternative posture selection rule has to be in effect for pointing movements.

The aim of Chapter 5 was to determine if motor primitives would provide such a posture selection rule for pointing movements. For this purpose, a randomised pointing task was created in a virtual environment. Participants had to point to virtual target locations within the work range of the arm. Results showed that arm postures in a three-dimensional target space can be reduced to three motor primitives. Thus, the number of independent degrees of freedom in a pointing task matches the dimensionality of the target space. This finding indicates that motor primitives result in a unique solution to the transformation between target position and posture. Therefore, motor primitives constitute a stand-alone rule for posture selection in pointing tasks, which can supersede other posture selection rules like sequential effects.

The work presented in this thesis investigated different rules for posture selection. The transfer of these rules to a continuous task space delivered new insights into the posture selection process (Chapter 2). A new hypothesis was proposed that can explain the observed motor behaviour in both binary and continuous posture selection tasks (Chapter 3). The same posture selection rules do not apply to every type of aimed limb movement (Chapter 4). When task demands are low, some selection rules can be superseded by more basic rules (Chapter 5). The implications of these results on the cognitive principles of posture selection are discussed in Chapter 6.

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